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A biosystematic study of the *Senecio streptanthifolius* Greene complex

by

(C) John F. Bain

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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IN

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled A biosystematic study of the *Senecio streptanthifolius* Greene complex submitted by John F. Bain in partial fulfilment of the requirements for the degree of Doctor of Philosophy

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Dedication

This thesis is dedicated to Laura Serven, who taught me that we cannot afford to measure our worth only by our apparent intelligence or by our accomplishments.

Abstract

A biosystematic analysis of the *S. streptanthifolius* complex has resulted in a major rearrangement of the taxa. Whereas recent treatments (Barkley 1962, 1978) have defined the complex as comprising one large polymorphic species, the present study divides it into seven taxa, five species and two varieties. The numerical analysis which included 32 structural characters and twelve flavonoid characters divided the OTUs into four major groups, two of which were further sub-divided after the inclusion of ecological and distributional data. These seven groups were used as the basis for describing the seven taxa recognized. The basic chromosome number of the *S. streptanthifolius* complex is x=23, the same as it is for most aureoid *Senecio* species; *S. kluanei* is the only strictly tetraploid (n=46) species, while *S. streptanthifolius* var. *rubricaulis* is comprised of both diploid and tetraploid populations. *Senecio laetiflorus, S. oodes, S. wallowensis, S. streptanthifolius* var. *streptanthifolius* and var. *borealis* are all predominantly diploid although occasional tetraploid populations have been recorded for the latter three taxa. A total of 35 flavonoid glycosides have been isolated and identified from 52 populations representing the *S. streptanthifolius* complex and related species. The pattern exhibited is one of complex glycosylation of a relatively small number of simple flavonoid molecules (quercetin, kaempferol, isorhamnetin, apigenin and luteolin). Flavonoid and structural characters were used to construct separate cladograms of the *S. streptanthifolius* complex. The two cladograms are nearly congruent; after re-evaluation of some characters, a combined cladogram was produced. The complex is considered to consist of two major clades, one combining *S. wallowensis* and *S. laetiflorus*. On the other clade speciation is postulated to have occurred twice via hybridization involving taxa outside the complex, producing *S. oodes* and *S. kluanei*. *Senecio streptanthifolius* var. *rubricaulis* is identified as a collection of introgressant populations between *S. streptanthifolius* and *S. multilobatus* with possible influence from other aureoid taxa. *Senecio streptanthifolius* var. *borealis* is considered to have invaded previously glaciated northern areas after the

Pleistocene and subsequently differentiated from var. *streptanthifolius*. *Senecio laetiflorus* and *S. wallowensis* arose from a common ancestor whose past distribution is thought to have included each of their present ranges. The overall variation pattern in the *S. streptanthifolius* complex suggests that speciation has occurred in stages, the first differentiation stage producing some taxa with a second hybridization stage producing more taxa with complex connections to the first group. This same pattern occurs throughout the aureoid complex. The taxa are of two major types; those that have achieved some genetic isolation via polyploidization, ecological or geographical isolation tend to be more homogeneous, structurally and presumably genetically, while those that are apparently not isolated by the above means are more variable.

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Steven Wolf and Louise Abele have been very supportive through thick and thin. Their faith has been very helpful and is greatly appreciated. Generations of fellow graduate students have all played an important role in my education. I owe them all a great deal. My parents' ability to convince me that what I was doing was worthwhile helped me to finish the task.

Finally, my attempts to express my appreciation to Joann will I fear always fall short of the mark. Hopefully she's gotten the message somehow.

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I. Introduction

The genus *Senecio* L. is one of the largest, most cosmopolitan plant genera in the world. It is estimated to comprise as many as 3000 species (Nordenstam, 1978) and its distribution includes all continents except Antarctica. The species assume diverse habits, from herbaceous to arborescent. The tribe Senecioneae, of which *Senecio* is the largest member genus, can be characterized as having inflorescences mostly radiate, phyllaries mostly uniseriate, and pappi of capillary bristles. Traditionally (Bentham, 1873; Bentham & Hooker, 1873) the tribe has been divided into four sub-tribes; the Senecioneae (*ca.* 1150 species - estimates derived from Bentham, 1873), the Liabinae (*ca.* 40 species), the Tussilagininae (*ca.* 20 species), and the Othonninae (*ca.* 150 species). Recently Nordenstam (1977) has raised the Liabinae to tribal rank, merged the Tussilagininae and the Othonninae with the Senecioneae to form one large 'natural' subtribe and described a new subtribe, the Blennospermatinae. The latter is "more of a gathering of problematic genera with obscure affinities" (Nordenstam, 1977) than a natural assemblage.

Chemically the Senecioneae is characterized by the presence of pyrrolizidine alkaloids (restricted to two tribes in the Compositae: the Eupatorieae and the Senecioneae) and furanoeremophilane sesquiterpine lactones, which are unique to the Senecioneae. In addition, the tribe Senecioneae is one of two tribes (the other being the Cichorieae) where polyacetylenes are scarce (Sorensen, 1977).

Although there are approximately 100 genera in the tribe (sensu Nordenstam, 1977), the single genus *Senecio* accounts for most of the over 3000 species in the tribe. *Senecio* (sensu Bentham, 1873) can be distinguished from other genera in the tribe by having flattened style branches with truncate, penicillate apices and ventro-marginal, discrete stigmatic lines. Nordenstam's stricter definition included only those species which, in addition, have basally enlarged filament collars, where the uppermost portion of the stamen filament is dilated and is composed of larger cells, and endothecial cells with usually numerous thickenings on vertical walls. In the latter the fibrous layer or

endothecial tissue of the anther wall exhibits ribs or thickenings along the inner vertical cell wall. Excluded species are included in a number of segregate genera (Nordenstam, 1978).

Taxonomic Summary of Senecio

The most recent world wide monograph of the genus was provided by De Candolle in his *Prodromus* in 1838. He recognized 596 species and placed them into sixteen series bearing names such as *Australasici, Madagascariensis, Brasiliensis,* and *Boreali-americani*. As their names suggest they were separated to a large degree on differences in geographical distribution. Bentham (1873) attempted to divide the genus into sections based on structure but, found he could not do so with any assuredness and so adopted De Candolle's geographical criterion. Recent attempts to divide the genus into more manageable groups have concentrated on splitting *Senecio* into multiple genera rather than into sections within the genus. These studies have used mainly structural criteria. Robinson and Brettell (1973 a,b,c) in their studies of the 'Cacalioid' group in the Senecioneae relied heavily on the lack of specialized anther collars and the presence of fused stigmatic lines to define the Cacalioid species. In this way a number of *Senecio* species were transferred to new Cacalioid genera. Nordenstam (1978) relied on similarly microscopic characters such as filament collar fine structure and ovary wall crystals to establish new genera, while Jeffrey *et al.* (1978) restricted themselves to sixteen comparatively easy to observe characters to group species into three major series composed of a total of sixteen 'groups', further divided into a total of 62 clusters. The latter authors went on to suggest that the name *Senecio* should apply to only one of the sixteen groups and that the other fifteen should be placed in other new or existing genera.

All of the world-wide, non-monographic treatments (Bentham, 1873; Jeffrey *et al.*, 1978; Nordenstam, 1978) of *Senecio* maintain the North American species within *Senecio (sensu stricto)*. When, however the species are examined from a more restricted North American perspective some

disagreement exists regarding generic and infrageneric boundaries. Three major synthetic treatments of *Senecio* in North America have been produced, the first by Asa Gray in 1843, the second by J.M. Greenman from 1915 to 1918, and the third by T.M. Barkley in 1978. These treatments range from the very conservative "lumping" of Asa Gray to the extreme "splitting" of J.M. Greenman. Gray recognized ten species groups and only 40 species, including the polymorphic *S. aureus* L. Greenman recognized a total of 22 sections in two subgenera. Finally, and most recently, Barkley recognized 10 species groups or sections and 105 species. By way of comparison, Greenman completed only 8 of his proposed 22 sections and by then had already recognized 131 species.

The first recognition of what has been most recently referred to as the **aureoid complex** (Barkley, 1978) was made by Gray (1843), who subdivided *S. aureus* L. into five varieties and recognized *S. elliottii* (*S. obovatus*), *S. tomentosus*, and *S. canus* in the same species group. Gray's use of this broad species concept for *S. aureus* was opposed by other workers, most notably E. L. Greene who described, from within the boundaries of Gray's *S. aureus*, 12 distinct species, some of which are mentioned in Table 1. Table 2 consists of a complete listing of aureoid species described by Greene. Greene did not arrange species into sections or groups whereas Greenman, whose species concepts were similar to Greene's, did. Greenman recognized 47 species in the section *Aurei*, which was roughly analagous to Gray's *S. aureus*, *S. elliottii*, and *S. resedifolius*. A comparison of Greenman's treatment of sect. *Aurei* to those Gray (1843) and Barkley (1978) appears in Table 1. The section *Aurei* was first described by Rydberg (1900) along with the sections *Lobati*, *Tomentosi* and *Subnudi*. Greenman later adopted three of the sections, uniting the fourth (section *Subnudi*) with section *Aurei*. It is important to note that in Rydberg's original paper (1900) he makes clear that "the four groups are closely related and grade into each other." So we see that from their inception, the sections *Aurei*, *Tomentosi*, and *Lobati*, were not thought to be easily separable. In this way Rydberg concurs with Gray's original grouping of *S. canus* and *S. tomentosus* (sect. *Tomentosi*) together with *S. aureus* (sect. *Aurei*).

Table 1. A comparison of classifications for *Senecio* sect. *Aurei*

Gray (1843)	Greenman (1916)	Barkley (1978)
S. elliottii T.&G.	*S. obovatus* Willd.	*S. obovatus* Willd.
	S. cymbalarioides Nutt.	
	S. platylobus Rydb.	
	S. aquariensis Greenm.	
	S. farriae Greenm.	
	S. willingii Greenm.	*S. streptanthifolius* Greene
	S. laetiflorus Greene	
	S. suksdorfii Greenm.	
	S. rubricaulis Greene	
	S. wardii Greene	
	S. pammelii Greenm.	
	S. pauperculus Michx.	
	S. gaspensis Greenm.	
	S. crawfordii Britt.	*S. pauperculus* Michx.
	S. flavovirens Rydb.	
S. aureus L.	*S. multnomensis* Greenm.	
	S. tridenticulatus Rydb.	
	S. acutidens Rydb.	*S. tridenticulatus* Rydb.
	S. aureus L.	*S. aureus* L.
	S. fedifolius Rydb.	*S. debilis* Nutt.
	S. debilis Nutt.	
	S. plattensis Nutt.	*S. plattensis* Nutt.
	S. schweinitzianus Nutt.	*S. schweinitzianus* Nutt.
	S. pauciflorus Pursh	*S. pauciflorus* Pursh
	S. crocatus Rydb.	*S. crocatus* Rydb.
	S. porteri Greene	*S. porteri* Greene
	S. indecorus Greene	
	S. burkei Greenm.	*S. indecorus* Greene
	S. idahoensis Rydb.	

S. subnudus D.C.	*S. subnudus* D.C.	*S. cymbalarioides* Buek
	S. fernaldii Greenm.	
S. resedifolius Less.	*S. resedifolius* Less.	*S. cymbalaria* Pursh
	S. ovinus Greene	
	S. conterminus Greenm.	
	S. quarens Greene	*S. quarens* Greene
	S. dimorphophyllous Greene	*S. dimorphophyllous* Greene
	S. hartianus Heller	*S. hartianus* Heller
	S. smallii Britt.	*S. anonymous* Wood
	S. hyperborealis Greenm.	*S. hyperborealis* Greenm.
	S. newcombei Greene	*S. newcombei* Greene
	S. cardamine Greene	*S. cardamine* Greene
	S. pseudaureus Rydb.	*S. pseudaureus* Rydb.
S. canus Hook.	*transferred to*	*transferred to*
S. tomentosus Michx.	*sect. Tomentosi*	*sect. Tomentosi*
	S. hesperius Greene	
	S. rosei Greenm.	
	S. soldanella Gray	
	S. cyclophyllus Greenm.	
	S. quebradensis Greenm.	
		S. ganderi Barkley & Beauchamp
		S. layneae Greene
		S. clevelandii Greene

Table 2. A summary of the subsequent treatment of the aureoid *Senecio* species described by E. L. Greene.

Species Name	Year Published	Revision Authors	
		Greenman (1916)	Barkley (1978)
actinella	1883	+	+
austinae	1885	+	–
blumeri	1909	–	–
cardamine	1881	+	+
chapacensis	1909	?	–
clevelandii	1883	?	+
cognatus	1900	–	–
densus	1900	–	–
dileptiifolius	1902	?	–
dimorphophyllous	1900	+	+
encelia	1909	–	–
flavulus	1900	–	–
franciscanus	1889	+	+
indecorus	1897	+	+
ionophyllous	1889	+	+
laetiflorus	1896	+	–
lamberti	1896	–	–
layneae	1883	?	+
lynceus	1895	+	–
mogollonicus	1906	?	–
ovinus	1900	+	–
pentodontus	1901	–	–
petrocallis	1900	–	–
petrophilus	1897	–	–
porteri	1897	+	+
prionophyllous	1906	–	–
pyrrochrous	1901	–	–
quarens	1906	+	+
quercetorum	1909	+	+
rubricaulis	1896	+	–
streptanthifolius	1895	–	+
stygius	1909	+	–
tidestromii	1897	–	?
toumeyi	1898	–	–
valerianella	1900	?	+
wardii	1900	+	–
species recognized/total		**16/36**	**13/36**

\+ = recognized as a valid species
\- = placed in synonomy
? = not mentioned.

It is essentially this view that Barkley adopted in 1978 when he used the term "aureoid complex" in an all-encompassing manner and abandoned formal recognition of the sections *Lobati*, *Tomentosi*, *Aurei*, *Bolanderi*, and *Sanguisorboidei*; referring to them instead as the "species groups" *Lobati* (including sect. *Bolanderi*), *Tomentosi*, and *Aurei*. The *Sanguisorboidei*, because it is largely made up of Mexican species was not affected by Barkley's "north of Mexico" treatment. Those species of the section which do occur in the southern United States were transferred to the *Lobati* or the *Annui* (because they are annuals). The distribution of the aureoid complex (*sensu* Greenman, Rydberg and Barkley) is shown in Figure 1. The complex extends from Alaska to southern Mexico in the west and from southern Newfoundland to Florida in the east. With a few exceptions, it does not extend much above 50°latitude in eastern Canada. In Mexico the distribution follows closely the range of the Sierra Madre Orientale.

The aureoid complex was further recognized to be a single and distinct entity by Löve & Löve (1976) who in this and a subsequent paper (Weber & Löve, 1981) transferred most of the species of the aureoid complex to the segregate genus *Packera*. The genus was recognized largely by its distinct base chromosome number of x=23. Although structural criteria were also cited the genus has not met with wide acceptance.

Biosystematic studies within the Aureoid complex

After Greenman's monograph very little research of a biosystematic nature was carried out on *Senecio* in North America until the early 1960's, when various surveys of chromosome numbers in *Senecio* and related Compositae were published (Ornduff *et al.*, 1963, 1967; Palmblad, 1965; Turner *et al.*, 1961, 1962). The emergence of x=23 as the base number for a number of species in the aureoid complex was noted with interest by Ornduff *et al.* (1963). Around this time, Barkley (1962) published a revision of Greenman's section *Aurei*, drawing attention to the apparent intergradation of many species

Figure 1. The distribution of aureoid *Senecio* species in North America.

170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
120
110
100
90
80
NORTH AMERICA
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
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in the aureoid complex. Both these characteristics of the complex have attracted the attention of subsequent workers.

Numerous gametic chromosome numbers have been reported in *Senecio* (n=5,9,10,19,20,21,23,24,30,38,40,45,50,52,65,90; Federov, 1969). The base number for the genus was originally thought to be x=5 (Afzelius, 1949) but more recently x=10 has been considered to be the true base number (Ornduff *et al.*, 1963; Nordenstam, 1977). Thus the x=23 base in the aureoid complex is obviously of polyploid origin. Barkley (1962) suggested that the resulting "genetic redundancy" is one of the factors which allows for the high degree of hybridization which occurs in the group. Numerous meiotic irregularities, including univalents, rings, chains and B-chromosomes have been reported (Ornduff *et al.*, 1967; Morton, 1981). Another common chromosome number within the aureoid complex is n=22. It is found far more commonly in eastern North American taxa where polyploids based on n=22 are also found (see Table 3). In addition, two aureoid species, *S. pseudaureus* and *S. flettii* have documented chromosome numbers based on x=20. Just what their relationship is to the rest of the complex is at present unknown.

Citing structural and distributional data as evidence, Barkley (1968a) reported the existence of intergradation between sections *Aurei*, *Tomentosi*, and *Lobati* through *S. mutabilis*. The other species involved were *S. tridenticulatus* (sect. *Aurei*), *S. multilobatus* (sect. *Lobati*), and *S. neomexicanus* (sect. *Tomentosi*). In a later paper (Barkley, 1980), he added *S. streptanthifolius* to the list of species involved in the intergrading complex.

In eastern North America, Kowal (1975) has presented a detailed analysis of the *S. aureus* complex on the Gaspé peninsula. He used a combination of techniques including chromosome analysis, breeding system studies, standard environment transplant experiments and computer analysis of a large number of structural characters. After combining all of his results he concluded that although hybridization did take place on the Gaspé peninsula, it was restricted to *S. aureus* and *S. pauperculus* and occurred only in open habitats, with the resulting hybrid populations being very localized. He further concluded that

Table 3. Previously reported chromosome numbers in *Senecio*

Taxon	n=	Locality	Reference
S. anonymous Wood	22	NC: Avery Co.	Ornduff, *et al.*(1967)
		NC: Durham Co.	Kowal (1975)
		NC: Nash Co.	Kowal (1975)
		NC: btwn Rutherfordton & L. Lure	Morton (1981)
		SC: Jackson Co.	Ornduff, *et al.*(1967)
		SC: Lancaster Co.	Ornduff, *et al.*(1967)
		SC	Jones (1968)
		GA: Walnut Grove Co.	Chapman & Jones (1971)
		TN: btwn La Vergne & Smyrna	Morton (1981)
S. antennariifolius Britt.	23	PA	Palmblad (1965)
S. aureus L.	22	MD: Montgomery Co.	Kovanda (1978)
		NC: Mitchell Co.	Ornduff, *et al.*(1967)
		NC: Wautauga Co.	Ornduff, *et al.*(1967)
		NC: Allegheny Co.	Ornduff, *et al.*(1967)
		NY: Tompkins Co.	Kowal (1975)
		PQ: Gaspé	Kowal (1975)
	2n=44	ONT: L. Superior	Morton (1981)
		NC: L. Lure	Morton (1981)
	2n=44+2b	VA: Wise Co.	Morton (1981)
	66	PQ: Gaspé	Kowal (1975)
		PQ: Gaspé	Kowal (1975)
	66+6b	ONT: 30 mi. E of Wawa	Morton (1981)
	2n=ca.130	ONT: Manitoulin Is.	Morton (1981)
S. bernardinus Greene	23	CA: San Bernardino Co.	Ornduff, *et al.*(1963)
S. bolanderi A. Gray	23	OR: Curry Co.	Palmblad (1965)
(*S. harfordii* Greenm.)	23	OR: Multnomah Co.	Palmblad (1965)

S. breweri Davy	23	CA: Los Angeles Co.	Ornduff, *et al.*(1963)
S. canus Hooker	23	OR: Josephine Co.	Ornduff, *et al.*(1963)
	ca.46	CA: Mono Co.	
		OR: Deschutes Co.	Strother (1972)
		OR: Clatsup Co.	Ornduff, *et al.*(1967)
		OR: Grant Co.	Ornduff, *et al.*(1967)
		OR: Wheeler Co.	Ornduff, *et al.*(1967)
		OR: Harney Co.	Palmblad (1965)
		ID: Custer Co.	Ornduff, *et al.*(1967)
		ID: Kootenai Co.	Ornduff, *et al.*(1967)
		CA: Inyo Co.	Ornduff, *et al.*(1967)
		WY: Albany Co.	Hartman (1977)
		MO: Carbin Co.	Ornduff, *et al.*(1967)
	46	CA: Siskiyou Co.	Ornduff, *et al.*(1963)
		CA: Siskiyou Co.	Taylor & Brockman (1966)
		CA: Shasta Co.	Palmblad (1965)
		OR: Wallowa Co.	Palmblad (1965)
	ca.48	NE: Elko Co.	Ornduff, *et al.*(1963)
	69	NE: Elko Co.	Taylor & Brockman (1966)
			Ornduff, *et al.*(1963)
	2n=ca.90	CO: Mt. Evans	Morton (1981)
	2n=ca.132	ALTA: Kananaskis	Morton (1981)
	46	BC	Ornduff, *et al.*(1967)
	69(+ca.69)	ALTA	Ornduff, *et al.*(1967)
	69		Taylor R.L. (1967)
S. clevelandii Greene	23	CA: Napa Co.	Ornduff, *et al.*(1963)
		CA: Colusa Co.	Ornduff, *et al.*(1967)
S. cymbalaria Pursh	2n=46	USSR: Altai	Sokolovskaja & Strelkova (1938)
	2n=46,ca.90	USSR: Sayona	Krogulevish (1978)
	2n=46	USSR: Sayona	Krogulevish (1976)
	2n=92	AK: Ogotoruk Creek	Johnson & Packer (1968)
	2n=92	USSR: Chukotka	Zhukova & Petrovsky (1975,1976)
(S. ogotorukensis Packer*)*	2n=46	AK: Ogotoruk Creek	Packer (1972)
		YT: Kluane L.	Packer (1972)
		YT: Ogilvie Mtns.	Packer (1972)
(S. fernaldii Greenm.*)*	138	NFLD: Table Mtn.	Packer (1972)
	ca.74-109	PQ: Gaspé	Kowal (1975)

(S. conterminus Greenm.)	2n=160+	ALTA: Waterton	Packer (1972)
S. cymbalarioides Buek.	2n=46	ALTA: Waterton Pk.	Packer (1972)
		WY: Park Co.	Packer (1972)
(v. moresbiensis)	2n=ca.88	BC: Queen Charlotte Is.	Morton (1981)
(v. moresbiensis)	2n=ca.90	BC: Queen Charlotte Is.	Taylor & Mulligan (1968)
S. dimorphophyllous Greene	ca.20	CO	Barkley (1962)
	ca.22(2n=ca.44)	CO: Lake Co.	Ornduff, *et al.*(1967)
S. eurycephalus (T.&G.) Gray	23	CA: Sonoma Co.	Ornduff, *et al.*(1963)
		CA: Modoc Co.	Ornduff, *et al.*(1963)
		CA: Napa Co.	Ornduff, *et al.*(1963)
		OR: Klamath Co.	Palmblad (1965)
S. flettii Weigand	20	WA: Clallam Co.	Palmblad (1965)
S. fendleri A. Gray	23	CO: Larimer Co.	Hartman (1977)
		CO: Fremont Co.	Keil & Steussy (1977)
		CO: Gunnison Co.	Ornduff, *et al.*(1967)
		WY: Albany Co.	Ornduff, *et al.*(1967)
	2n=46	CO: Mt. Evans	Morton (1981)
S. franciscanus Greene	23	AZ:Coconino Co.	Keil & Pinkava (1976)
S. greenei A. Gray	20–23	CA: Napa Co.	Ornduff, *et al.*(1963)
	46	CA: Lake Co.	Ornduff, *et al.*(1967)
S. hesperius Greene	23	OR: Josephine Co.	Ornduff, *et al.*(1963)
S. hyperborealis Greenm.	2n=46	NWT: Mackenzie Delta	Packer (1972)

S. indecorus Greene	n=88-92	PQ: Gaspé	Kowal (1975)
	2n=ca 126	ALTA: Columbia Icefield	Morton (1981)
	2n=ca 180	WY: Sheridan Co.	Morton (1981)
		YT: Rancheria R.	Morton (1981)
S. ionophyllous Greene	23	OR: Clackamas Co.	Ornduff, *et al.*(1963)
S. layneae Greene	46	CA: Eldorado Co.	Ornduff, *et al.*(1967)
S. macounii Greene	23	WA: San Juan Co.	Palmblad (1965)
	46	OR: Clackamas Co.	Ornduff, *et al.*(1963)
		OR: Wasco Co.	Ornduff, *et al.*(1963)
S. millelobatus Rydb.	23	AZ: Yavapai Co.	Ornduff, *et al.*(1967)
		AZ: Coconinno Co.	Ornduff, *et al.*(1967)
	24	AZ: Yavapai Co.	Ornduff, *et al.*(1963)
S. multilobatus T. & G.	23	WY: Uinta Co.	Hartman (1977)
		UT: Grant Co.	Keil & Stuessy (1977)
		UT: Iron Co.	Ornduff, *et al.*(1967)
		AZ: Coconinno Co.	Keil & Stuessy (1977)
		CA: Inyo Co.	Ornduff, *et al.*(1967)
		CO: Rio Blanco Co.	Ornduff, *et al.*(1967)
(S. uintahensis Greenm.*)*	2n=46	UT: E. of Cedar City	Morton (1981)
		AZ: Apache Co.	Ornduff, *et al.*(1967)
(S. uintahensis Greenm.*)*	46	NV: Elko Co.	Ornduff, *et al.*(1967)
S. neomexicanus A. Gray	23	AZ: Gila Co.	Ornduff, *et al.*(1963)
		AZ: Coconinno Co.	Keil & Stuessy (1977)
		UT: Grant Co.	Keil & Stuessy (1977)
	2n=44	AZ: Gila Co.	Morton (1981)
	2n=46	AZ: Greenlee Co.	Morton (1981)
		CO: Conejos Co.	Ornduff, *et al.*(1967)
		UT: San Juan Co.	Ornduff, *et al.*(1967)
	48	AZ: Greenlee Co.	Morton (1981)

S. newcombii Greene	24	BC: Queen Charlotte Is.	Taylor & Mulligan (1968)
S. obovatus Muhl. *ex* Willd.	22	KS: Douglas Co.	Jackson, R.C. (1962)
		NY: Washington Co.	Kowal (1975)
	2n=44	OH: N. of Cincinnati	Morton (1981)
	ca.90	ONT: Manitoulin Is.	Morton (1981)
S. pauciflorus Pursh	87-92	PQ: Gaspé	Kowal (1975)
	2n=ca.130	YT: Dawson	Morton (1981)
S. pauperculus Michx.	22	PQ: Gaspé	Kowal (1975)
		ALTA	Ornduff, *et al.*(1967)
		OR: Lake Co.	Strother (1972)
	23	BC	Ornduff, *et al.*(1963)
		WA: Kittatas Co.	Ornduff, *et al.*(1963)
		WA: Kittatas Co.	Palmblad (1965)
	44	NY: Genesee Co.	Kowal (1975)
	ca.44	NC: Durham Co.	Kowal (1975)
	46	ALTA	Ornduff, *et al.*(1963)
		ALTA	Ornduff, *et al.*(1967)
	2n=40	YT: Koidern	Morton (1981)
	2n=ca.40	NFLD: St. Anthony	Morton (1981)
		SD: Black Hills	Morton (1981)
	2n=42	ONT: Bruce Peninsula	Morton (1981)
	2n=44	BC: N. of Ft. Nelson	Morton (1981)
		ALTA: Jasper Pk.	Morton (1981)
		ONT: Kingston	Morton (1981)
		PQ: Megantic Co.	Morton (1981)
		NFLD	Morton (1981)
		WY: Bighorn Mtns.	Morton (1981)
	2n=ca.46	ONT: L. Superior	Morton (1981)
	2n=64	NFLD: Peninsula	Morton (1981)
	2n=ca.84	MT: Roseau Co.	Morton (1981)
	2n=ca.88	ALTA: Banff-Jasper Pk.	Morton (1981)
		MAN: Red Deer L.	Morton (1981)
	2n=ca.90	MAN: Red Deer L.	Morton (1981)

S. plattensis Nutt.	ca.46	KS: Scott Co.	Kowal (1975)
S. pseudaureus Rydb.	20	WA: Kittatas Co.	Palmblad (1965)
	40	OR: Wallowa Co.	Palmblad (1965)
	ca.20(2n=ca.40)	ID: Custer Co.	Ornduff, *et al.*(1967)
		BC: Cathedral Pk.	Morton (1981)
S. sanguisorboides Rydb.	2n=46 ±2	NM: Santa Fe Co.	Ornduff, *et al.*(1967)
S. schweinitzianus Nutt.	22	PQ: Carleton	Kowal (1975)
	23	Swed. Bot. Gard.	Palmblad (1965)
S. streptanthifolius Greene	23	WA: Kittatas Co.	Ornduff, *et al.*(1963)
		CA: Nevada Co.	Ornduff, *et al.*(1967)
		CA: Siskiyou Co.	Ornduff, *et al.*(1963)
		CO: Lake Co.	Ornduff, *et al.*(1967)
		BC: Natal	Taylor & Brockman (1966)
	2n=46	ALTA: Livingston Falls	Morton (1981)
	2n=ca.90	WY: Sheridan Co.	Morton (1981)
S. tomentosus Michx.	23	NC: Franklin Co.	Ornduff, *et al.*(1967)
		SC: Lancaster Co.	Ornduff, *et al.*(1967)
	2n=46	GA: Atlanta	Morton (1981)
S. tridenticulatus Rydb.	23	NM: Colfax Co.	Ornduff, *et al.*(1967)
		CO: Fremont Co.	Keil & Stuessy (1977)
		CO: Kit Carson Co.	Keil & Stuessy (1977)
S. werneriaefolius A. Gray	22	CO: Rocky Mtn. Nat'l. Pk.	Weins & Halleck (1962)
	23	CO: Inyo Co.	Ornduff, *et al.*(1967)

recognition of *S. gaspiensis* as distinct from *S. pauperculus* was unwarranted.

Chapman and Jones (1971) have reported the existence of hybrids between *S. smallii* (sect. *Aurei*) and *S. tomentosus* (sect. *Tomentosi*) where their distributions overlap on the granitic flatrocks of the southeastern United States Piedmont. *Senecio smallii* has a chromosome number of n=22 while *S. tomentosus* is n=23. Meiosis in the hybrid is abnormal with between one and three univalents being formed and with a resultant reduction in stainable pollen. As was the case in Kowal's study, they found that once again the hybridization was not followed by introgression.

Packer (1972) used data from cytology, morphology, (including pollen structure) and phytogeography in his study of the arctic and alpine aureoid *Senecio* species. He found a wide range of ploidy levels which were constant within each species and no evidence for hybridization.

With regard to breeding systems, Barkley (1962) concluded from observations within the sect. *Aurei*, that isolated individuals are likely to produce reduced quantities of seed. He therefore believed the *Aurei* to be normally cross-pollinated. Kowal (1975) reported the majority of species he examined to be self-sterile. Only the related discoid octaploid species, *S. indecorus* and *S. pauciflorus* were found to be self-fertile. No evidence for apomixis in the genus has ever been reported (Nordenstam, 1977).

Few if any chemosystematic studies of North American *Senecio* species have been reported. There are indications that such studies would prove fruitful from the work of Glennie *et al.* (1971). In this study the authors were able to correlate flavonoid chemistry and plant geography in the *Senecio radicans* complex. They identified two flavones, apigenin 7-glucoside and 6,8 di-C-rhamnosylapigenin, and five flavonols, quercetin and kaempferol 3-glucoside, quercetin and kaempferol 3-rutinoside and the much rarer quercetin 3-methyl ether. In one species they also found the C-glycosyl xanthones mangiferin and isomangiferin. As well as having been used in *Senecio*, flavonoid profiles have been successfully used in other western North American taxa for studying taxonomic and phytogeographic problems (*e.g.* Wolf, 1981).

Where taxonomic boundaries are extremely difficult to discern sometimes computer assisted numerical taxonomy is useful in solving such problems. The fundamental position of numerical taxonomy (as stated by Sokal and Sneath, 1973) is that classifications are based on phenetic similarity, and that the quality of the classification increases with the number of equally weighted characters used. Although numerical aids have been used sparingly in aureoid *Senecio* taxonomy, species have always been defined on a strictly phenetic basis and as such, are readily amenable to numerical analysis.

The aureoid complex presents a formidable number of taxonomic problems which have yet to be unravelled. *S. streptanthifolius*, or more precisely, the *S. streptanthifolius* species group was chosen for the present study for a number of reasons. The aureoid complex as a whole presented too large a problem to undertake in the current timeframe so a more restricted study was defined, which at the same time would provide a broad foundation for further study within the complex. Barkley (1978) characterized *S. streptanthifolius* as "an unusually complex species with several weakly defined phases having conspicuous extreme forms. It intergrades morphologically with nearly every other aureoid *Senecio* with which it shares overlapping ranges, most notably *S. pauperculus*, *S. tridenticulatus*, *S. multilobatus*, *S. neomexicanus*, and *S. canus*." In addition Barkley stated that "*S. pauperculus* and *S. streptanthifolius* collectively form an intergrading plexus through which nearly all other aureoid senecios are eventually connected." In a previous more detailed treatment of *S. streptanthifolius*, Barkley (1962) stated that the species "encompasses several more or less divergent phases, each of which is characterized by its own aspect, which relates to a series of morphological tendencies." He went on to discuss the phases, each of which is associated with at least one species name which had been recognized in Greenman's treatment. It is clear that Barkley recognized the structural diversity within *S. streptanthifolius*, even to the point where he could associate a name with most of the phases, and yet he felt that the variation was sufficiently continuous as not to merit taxonomic recognition. Kowal (1975) found this same situation in

the *S. aureus* complex on the Gaspé peninsula and it is this same pattern of intergrading diversity which makes the majority of the aureoid species so difficult to define.

The structural variation having been thus documented, the next step is to ascertain whether the variation has a genetic basis or whether it is attributable to environmental factors. Also important is the assessment of the extent to which hybridization and/or introgression is responsible for the observed variation. In addition it is important to examine the patterns of variation in light of how they might be best explained by past phytogeographic and historical events. Kowal (1975) has already demonstrated that standard environment experiments can be useful in this type of study. Growing of the phases of *S. streptanthifolius* from seed under identical, controlled conditions should not only give insight into the amount of variation that is environmentally controlled, but should also provide information about the life history of the plants. The possibility for conducting artificial crossing experiments with the plants being grown under artificial conditions also exists.

The use of flavonoid chemistry in hybridization studies is well documented (Smith and Levin, 1963; Alston and Turner, 1963; Taylor, 1972; Crawford, 1972; King, 1977; Umber, 1980). *Senecio streptanthifolius*, since it appears to intergrade with a number of other aureoid species, would seem to be a natural subject for flavonoid study from this standpoint especially since it has been unclear in the past whether the intergradation was due to hybridization and introgression or whether it was due merely to structural plasticity (Barkley, 1962). Most of the phases described by Barkley have well defined distribution patterns, and as previously mentioned, Glennie *et al.* (1971) have used flavonoid analysis to advantage for insight into the phytogeographical patterns in another *Senecio* species complex. *S. streptanthifolius* presents some interesting if somewhat subtle phytogeographic problems relating to its phases which possibly could be solved by a similar flavonoid study.

The occurrence of polyploidy within *S. streptanthifolius* was alluded to by Barkley(1962) when he reported the findings from a preliminary study of

pollen grain size. This has not been pursued as yet. Polyploidy has already been documented in the aureoid complex (Ornduff *et al.*, 1967; Packer, 1972), and associated with speciation (Packer, 1972). A thorough cytotaxonomic survey of the *S. streptanthifolius* complex would provide valuable information regarding the disposition of the phases in the complex.

Part of the difficulty in separating taxa within the aureoid complex arises because of the importance attached to leaf characters. Both Barkley (1978) and Greenman (1916) rely heavily on leaf characters in their keys and yet they note intra-specific character variability in the text of their descriptions. The employment of modern numerical methods with an increased number of characters will aid in testing and refining the taxonomic boundaries as they are currently defined within the *S. streptanthifolius* complex. Not only would this provide for a more natural (*i.e.* neo-Adansonian *sensu* Gilmour, 1951 and Sokal and Sneath, 1973) taxonomy, but it would also, through various clustering techniques, give insight into the relative phenetic distances separating the taxa. One reason strict phenetics has been employed exclusively in the past is at least in part because it is difficult to assign plesiomorphous and apomorphous states to the leaf characters used so extensively. It is hoped that this study will provide flavonoid characters with known plesiomorphous and apomorphous states so that some insight into the phylogeny of the *S. streptanthifolius* complex may be obtained.

II. Materials and Methods

A. Morphology

Field collections of the *S. streptanthifolius* complex and of other aureoid *Senecio* species were made from throughout the complex' entire range. Collections from each locality included pressed specimens, air-dried bulk collections for flavonoid studies and either preserved buds or mature achenes for chromosome analysis. On the rare occasion where neither of the latter was available, live plants were collected and transported to the greenhouse facilities of the University of Alberta.

Structural and distributional studies were based on collections as outlined above as well as on herbarium specimens from the following herbaria:

University of Alberta (ALTA); National Academy of Sciences, Philadelphia (PH); British Museum (BM); Brigham Young University(BRY); National Museum of Canada, Ottawa (CAN); California Academy of Sciences (CAS); University of Colorado (COLO); Biosystematics Research Institute, Department of Agriculture (DAO); Dudley Herbarium (DS); Field Museum (F); Gray Herbarium of Harvard University (GH); Jepson Herbarium, University of California (JEPS); Missouri Botanical Garden (MO); University of Notre Dame (ND); Greene Herbarium, University of Notre Dame (NDG); New York Botanical Garden (NY); Oregon State University (OSC); University of Pennsylvania (PENN); Rocky Mountain Herbarium, University of Wyoming (RM); University of Texas (TEX); University of California, Berkeley (UC); U.S. National Herbarium (US); Intermountain Herbarium, Utah State University (UTC).

A total of 33 structural characters were chosen for scoring specimens for phenetic similarity. The characters were chosen based on previous authors' use (*i.e.* Greenman 1916, Barkley 1962,1978) and my experience in the field and the greenhouse. In the statistical analysis, only the thirty-two quantitative characters were used.

A number of leaf characters were obtained through the combined use of a Houston Instrument "Hipad" digitizer and a program written by Dr. Mark Dale of the University of Alberta. As well as calculating the leaf area, leaf

perimeter, basal leaf angle, maximum leaf width, the distance of the maximum width from the apex, the total leaf length, the ratio of these last two values and the ratio of leaf length to width, the program drew a polygon joining the outermost points of each leaf. It then calculated the area and perimeter of this polygon. Two ratios were then calculated: leaf area/polygon area and leaf perimeter/polygon perimeter. Each ratio is a measure of the entirety of a leaf although the two are inversely related. Leaves were scored by xeroxing the leaf shape onto a clear acetate sheet and then projecting the shape onto the digitizer through the use of an overhead projector and a mirror. The shape could then be accurately recorded, the magnification noted and the conversion factor calculated later.

The data collected were used in two separate analyses, a numerical analysis and a statistical analysis.

The numerical analysis was used to establish the clustering patterns of the specimens. These patterns were then used to aid in establishing taxa. At the same time the taxa outlined in the Historical Perspective section (see Results) were evaluated by comparison with the new clusters produced. The classification program used was TAXMAP, a program developed by Dr. J.W. Carmichael of the University of Alberta. This program calculates the ranges of the variables, normalizes the raw data as fractions of the range, then calculates a relative proximity between each pair of OTUs. It allows for the weighting of characters according to their relative information content (*i.e.* the number of classes), but this option was not exercised. All characters were weighted equally to minimize subjectivity. The clustering procedure in the program is outlined by Carmichael (1980) and the results are illustrated by means of a taxometric map (Carmichael and Sneath, 1969). This map is actually a two-dimensional representation of the multi-dimensional hyperspace in which the OTU's exist. Circles represent clusters (points are single member clusters) and lines joining them are the undistorted phenetic distances between clusters. Taxometric maps were drawn with the aid of the Calcomp plotter of the University of Alberta computing facilities and, where necessary, by hand.

The statistical analysis was conducted in order to evaluate the individual characters used in the numerical analysis so that those most useful for separating the taxa in the *S. streptanthifolius* complex could be identified. This was accomplished by conducting a non-parametric analysis of variance, specifically the Kruskal-Wallis test. This method was chosen over ANOVA (analysis of variance) because it was felt that the assumptions required for ANOVA (equal variances and normal distribution) could not be reliably satisfied. An initial ANOVA and test for variance equality was conducted with the result that over half of the characters did not satisfy the equal variance assumption. The loss of sensitivity which results from using the Kruskal-Wallis test instead of ANOVA (Sokal and Rohlf, 1981) was not important in this case since the purpose of the analysis was to identify the most useful characters for separating taxa. The significance level of the H-statistic produced by the Kruskal-Wallis test was used as a measure of this usefulness. Those characters with a significance level $<.05$ level were not considered useful while those with a $>.005$ significance level were considered the most useful. In addition, the mean, standard deviation, and range were calculated for each character (see Appendix 3 for a list of values). All computations were performed using the MIDAS statistical package and the University of Alberta computing facilities.

The manipulation of data gained from herbarium sheet labels was greatly facilitated by the use of the Stanford Public Information and REtrieval System (SPIRES), which is a generalized computer information storage and retrieval system. Information on the herbarium labels was categorized into various **elements**, (*i.e.* genus, species, collector, state, province, county, elevation, association, *etc.*), which were used to build a **record** of each specimen. The resulting file of **records** was then searched using the **element** names to direct the search. Thus extensive information of a taxonomic, geographic and oftentimes ecological nature could be sifted and correlated. In fact, the only limitations are those set by the information content of the herbarium label. Considerable use of this facility has been made throughout the

study.

B. Chromosome Numbers

Meiotic chromosome counts were made from immature capitula fixed in the field in modified Carnoy's fixative, (4 chloroform: 3 ethanol: 1 glacial acetic acid), and later transferred to a solution of 70% ethanol. Squashing and staining techniques used were those of Turner (1960). Floret buds were stained whole in iron-acetocarmine, pulverized on a microscope slide with a glass rod and squashed under a cover slip. Mitotic counts were made from root tips harvested from plants grown in the greenhouse either from seed or from field transplants. The methods used were those of Tijo and Levin (1950). Root tips were pretreated in 8-hydroxyquinoline for 2-3 hours at 14° C, washed in distilled water for 5 minutes and stained in 1% acetic orcein in 1N HCl (1:9) for 20 minutes. The root tips were then placed on a microscope slide in a drop of 45% acetic acid and squashed with a cover slip. Voucher specimens are deposited at the University of Alberta herbarium.

In some instances chromosome counts were augmented by guard cell measurements. Measurements were made along the length of the guard cell for eight populations of known chromosome number, four diploid and four tetraploid. In each population, anywhere from 20-70 cells were measured. For populations of unknown chromosome number, between 50-60 guard cell lengths were measured and the mean length of each population was compared with the total means of the diploid and the tetraploid populations respectively by means of a t-test. All statistics and measurements were done with the aid of BIOQUANT statistical package, used in conjunction with an Apple II computer, a HIPAD digitizer and a drawing tube.

C. Flavonoid Chemistry

An initial survey of the flavonoid profiles within the *S. streptanthifolius* complex was carried out in the following manner.

All collections of bulk material (52 populations) were ground to powder in a blender. A small amount of powder (approx. 0.5 gm.) from each population was combined with 2-3 ml. of 80% methanol in a test tube. The contents were shaken and left to stand for 48 hours. The extract was then analyzed by standard two-dimensional paper chromatography using BAW, (4:1:5 butanol-acetic acid-water:upper phase) and 15% acetic acid. Using this method, the flavonoids present in a population show up as spots in a 2-D profile. In order to aid identification, the spots' colours were recorded both before and after fuming with NH_4 (ammonia). The spots then were stained with Naturstoffreagens A in MeOH (NA) and the resulting colours noted.

After this survey a number of representative populations were selected for an exhaustive flavonoid analysis. The combined 2-D profiles of these populations encompassed all the flavonoid variation present in the survey so that a complete analysis of these populations allowed the identification of all flavonoids present. Care was also taken to ensure that these representative populations encompassed as wide a range of structural variation as possible. A list of all the populations examined appears in the Appendix.

For the exhaustive analysis, approximately 10-20 gm. (dry weight) of powdered leaves and stems were added to approximately 500 ml. of 85% methanol and extracted for 24 hours on a shaker. The procedure was repeated with 50% methanol, the two extracts were combined and reduced *in vacuo* to approximately 50 ml.

Chlorophylls, waxes, tannins and terpenoids were removed by partitioning with a three-volume excess of chloroform. Chromatography revealed that this chloroform fraction contained no flavonoids so that in all subsequent analyses it was discarded. Further partitioning with ethyl acetate was initially carried out according to the methods of Neuman *et al.* (1979); chromatography, however, revealed that the flavonoid content of the ethyl acetate fraction was identical to

that of the water fraction so this partitioning step was subsequently abandoned. Thus in most cases, only the water fraction remaining after the initial chloroform partitioning was further examined.

Flavonoid analysis was carried out in two steps. The first step was to separate the water fraction by the same standard paper chromatographic techniques used in the survey, the only difference being that eighteen sheets of Whatmann 3mm paper were run per population. Flavonoid spots were cut out and eluted in 80% methanol for twenty-four hours on a shaker. The extract was reduced to dryness either *in vacuo* or by letting the extracts stand overnight in beakers on a microscope slide warmer. These extracts were then purified on small columns (15cm. X 1cm. diam.) of Sephadex LH-20 using 100% methanol as the eluting solvent.

In the second step, these isolated flavonoids were identified using one dimensional descending chromatography as well as standard hydrolytic and spectral procedures. Rf's were determined on Whatman #1 MM paper in four solvent systems: BAW, 15% acetic acid, water and 80% phenol. Approximately 10 µ of a 10^{-3}M solution of Rutin, (quercetin 3-0-rutinoside) was used as a reference standard on each sheet.

Ultraviolet spectrophotometry was carried out on a Unicam SP 1800 using the procedures of Mabry *et al.* (1969) and Neuman *et al.* (1979). Scans of the compounds were recorded and compared with those obtained after the addition of diagnostic agents including sodium methoxide, aluminum trichloride (AlCl3), AlCl3 +10% HCl, sodium acetate (NaOAc) and NaOAc + Boric Acid.

Hydrolysis of the sugar component of the flavonoid was carried out by the addition of 5 ml. of 0.1N trifloroacetic acid followed by heating (100° C) in a water bath for 90 minutes. The mixture was then partitioned with ethyl acetate and both fractions were evaporated to dryness. The ethyl acetate fraction, containing the aglycone, was redissolved in 100% methanol and subjected to the same spectral analysis that was carried out on the glycoside. The acid-aqueous fraction, containing the sugars, was redissolved in 5 ml. water and evaporated to dryness three times to remove all traces of the acid and

was then chromatographed with standards on silica gel plates, (DC Fertigplatten S.1 G-25). The plates were run twice in ethyl acetate-isopropanol-water (65:22:11), air dried, sprayed with analine phthalate reagent and developed by heating at 100° C for 15-30 minutes.

III. Results

A. Morphology

Historical Perspective

In preparation for the morphological analysis an initial examination of herbarium specimens was carried out to gain an overall view of the structural variability within the complex. A number of related species were also examined to help establish the boundaries of the complex. Finally, an attempt was made, through the examination of type specimens, other cited specimens and pertinent literature to gain familiarity with the species limits established by other workers, primarily Barkley, Greenman and Rydberg. At the end of this survey, the specimens of the *S. streptanthifolius* complex were segregated into taxa based on structures easily observed on herbarium sheets and aided and influenced by the descriptions afforded by previous authors.

What follows is a brief description of the structurally distinct entities encompassed in *S. streptanthifolius* as it is currently treated, with notes outlining how these entities have been treated in the past. The intent of this discussion is not to outline every taxon which has been described from within the bounds of *S. streptanthifolius*, nor to suggest that the following taxa deserve formal recognition, but rather to describe only those major entities which have been recognized with some consistency in the past. A formal treatment of synonymy will follow in a later section.

Senecio streptanthifolius Greene

Senecio streptanthifolius is a glabrous perennial with obovate to widely obovate leaves. The margin of the upper half of the leaf is dentate with numerous (>5) teeth while the lower half is entire. Although Greenman (1916) relegated *Senecio streptanthifolius* to varietal status under *Senecio cymbalarioides* Nutt., Barkley (1962) raised it back to species rank to replace

the name *Senecio cymbalarioides* Nutt. which is a later homonym of *Senecio cymbalarioides* Buek. The distribution of this typical form of the species is wide-ranging, from southern British Columbia and Montana south to California and Colorado. Within this range most other taxa in the complex are also found.

Senecio cymbalarioides var. *borealis* Greenm.

More northern populations of *S. streptanthifolius*, (*Senecio cymbalarioides* Nutt.), have been separated as var. *borealis* by Greenman (1916). He described it as having mostly subspatulate to oblanceolate leaves and very reduced, cauline leaves. To this I would add that the leaf margins are entire except at the tip where there are 3-5 teeth. He gave as its distribution the area from arctic America to Wyoming and Utah. Although I agree with this circumscription, I must add that its distribution south of Montana is sparse, whereas north of Montana and east of the Rocky Mountains it totally replaces var. *streptanthifolius*. Some northern specimens referred by Barkley to *S. streptanthifolius* are considered in this study to be thick-leaved variants of *S. pauperculus*.

Field studies in the southern Yukon revealed another turgid-leaved entity very similar to var. *borealis* but with leaf margins serrate along most of perimeter rather than weakly dentate at the tip. This entity appears to extend south into British Columbia.

S. acutidens Rydb.

This name was used by Greenman (1916) and Rydberg (1900) for specimens with leaves more oblanceolate and margins more deeply dentate than typical *S. streptanthifolius*. Rydberg (1900) also stated that the leaves are thicker than those of *S streptanthifolius* (*S cymbalarioides*). Barkley (1978) treated *S. acutidens* as a synonym of *S. tridenticulatus*. I have used it here strictly for specimens with margins deeply serrate to serrate-dentate. Its general distribution is from southern Idaho into Wyoming and Montana.

S. rubricaulis Greene

This entity was recognized as a phase of *S. streptanthifolius* by Barkley (1962) and as a distinct species by Greene (1896) and Greenman (1916). All characterized it as having coarsely dentate leaves and as such, it relates to *S. acutidens* as the latter is envisioned in this study. I have used *S. rubricaulis* only for specimens where, in addition to coarsely dentate margins, the plants have leaves that are truly lobed, at least toward the bottom. *Senecio rubricaulis* occurs generally farther south than *S. acutidens*, reaching Nevada and Utah.

S. platylobus Rydb.

Barkley (1962) considers *S. platylobus* to be a very robust form of the "*rubricaulis* phase" occurring in and around the Wasatch mountains of Utah. Rydberg (1900) allied *S. platylobus* with *S. pseudaureus* . In addition to the large overall size and the large size of the cauline leaves the specimens are characterized by a comparatively poorly developed basal rosette.

S. leonardii Rydb.

This is a permanently tomentose taxon from Colorado which was placed in section *Tomentosi* by Greenman and in synonymy with *S. streptanthifolius* by Barkley. Barkley did, however, use this name to denote one of the distinct phases of *S. streptanthifolius*. He initially described two tomentose phases, the "*leonardii* phase" and the "*molinarius* phase", the latter being more densely tomentose. In a subsequent publication (Barkley, 1978) he placed *S. molinarius* in synonymy with *S. wernaerifolius* which, based on examination of the type specimen of *S. molinarius*, is a better placing of the name. However, since Barkley cited a specimen (Bethel, Willey and Clokey4391) other than the type as representative of the "*molinarius* phase", the transferring of *S. molinarius* to *S. wernaerifolius* does not imply that Barkley now feels that the "*molinarius* phase" is part of *S. wernaerifolius*. I have not been able to reliably separate specimens into these two phase categories and so I treat them as a single

entity. Besides pubescence, another trait which characterizes this taxon is the shallow, even dentation of the leaf margins.

S. laetiflorus Greene

This distinctive variety found growing in saline soils in eastern Oregon, northeastern California and adjacent Nevada has generally well developed pinnatisect cauline leaves and, when growing at lower elevations (where it is most commonly found), is taller than *S. streptanthifolius*. Its leaves are not as thick textured and its petioles are generally longer. Although the basal leaves vary greatly, they appear to be generally more elliptic or ovate than those of typical *S. streptanthifolius*. The inflorescence is also more loosely arranged.

S. suksdorfii Greenm.

Senecio suksdorfii has been referred to as a short subcaespitose, alpine or subalpine phase with more or less crenate, rotund basal leaves. Although this general description applies to the taxon as I recognize it, I find most specimens previously referred to as *S. suksdorfii* are more easily treatable as *S. streptanthifolius*. The specimens from the Wallowa Mountains of Oregon and those from the Mt. Rose area in Nevada make up the majority of ones I include under what was previously called *S. suksdorfii* . Their basal leaves are distinctly more widely obovate with more truncate bases and their petioles and flowering stalks are shorter than *S. streptanthifolius*.

In this initial survey, other related species, including *S. canus*, *S. pauperculus*, *S. cymbalarioides*, *S. neomexicanus*, *S. tridenticulatus* and *S. multilobatus* were also examined.

After the initial study of herbarium specimens, a total of eighty-five specimens were selected as **operational taxonomic units**, (subsequently referred to as OTUs). For the numerical analysis the specimens were chosen so that in addition to variability within the *S. streptanthifolius* complex being well

represented, specimens representative of related species outside the complex were also included in the analyses.

Numerical Analysis

Two major numerical analyses were performed. The first analysis used all structural and flavonoid characters with each character weighted equally. This analysis, because it used the most characters, had the greatest information content and therefore was considered to be the most accurate. A second analysis, using all of the available structural characters, was run and compared with the original combined analysis. A third analysis, which was run in an attempt to name clusters will be discussed later in the text.

The results of the first analysis, using all forty-four characters, are presented in Table 4. The resulting taxometric map appears as Figure 2. Eighteen clusters and twenty-one isolated OTUs are separated. The clusters can be briefly categorized as follows:

Clusters #1 and #12 contain short specimens with small leaf length/width ratios and glabrous achenes.

Clusters #3,#7,#9,#13,#15 are all characterized by specimens with large leaf length/width ratios and margins dentate only at the apex.

Cluster #4 contains specimens with highly dissected cauline leaves and with basal leaves generally entire at the apex.

Cluster #5 is very similar to Cluster #3 group, the difference being that specimens in Cluster #5 have smaller leaf length/width ratios.

Cluster #6 is related to Clusters #2 and #10 but with more highly dissected leaves and hirtellous achenes.

Clusters #8 and #11 contain specimens which are floccose-tomentose especially at the base of the involucre.

Cluster #14 specimens are similar to the Cluster #3 group except that they are lightly tomentose at the base of the involucre and have a more

Table 4. Taxmap showing cluster membership for Analysis #1

*Taxon names are taken from the Historical Perspective section and follow approximately the treatment of Greenman (1916).

MAP CLUSTER ANALYSIS:-THE SENECIO STREPTANTHIFOLIUS COMPLEX -ALL CHARACTERS

(MINIMUM NUCLEUS 0.159, MAXIMUM DROP 0.0236 BOTH ARE 100% OF NORMAL)
EQUALLY WEIGHTED ATTRIBUTES

CLUSTER NO.	OTU NOS	DIST BEST LINK	OTU BEST LINK	AVGOF NEW LINKS	DROP IN AVG.	FAR OTU	DIST FAR OTU	FLAG	TAXON & COLLECTOR
1	83								suksdorfii Peck 18055
	84	0.06							suksdorfii Williams 78-248
	85	0.07	84	0.087	0.025	83	0.11		suksdorfii Peck 18038
	82	0.09	84	0.103	0.016	85	0.11		strept. Kruckeberg 5501
	69	0.10	83	0.127	0.024	85	0.17		suksdorfii Heller 9896
	77	0.10	84	0.146	0.019	69	0.18		laetiflorus UC 335863
	74	0.10	77	0.166	0.020	69	0.19		laetiflorus Crum 1939
	44	0.11	82	0.163	-0.003	74	0.22		v. borealis 129
	48	0.08	44	0.194	0.030	83	0.26	1000	v. borealis 139
2	40								acutidens 107
	64	0.07							platylobus Jeffery s.n.
	66	0.07	40	0.082	0.015	64	0.09		acutidens Lingenfelter 73
	62	0.11	64	0.112	0.030	66	0.12		rubricaulis Crong & D 2115
	65	0.12	40	0.134	0.022	62	0.14		acutidens Williams 1758
	41	0.12	62	0.158	0.024	66	0.19		acutidens 108
	26	0.12	64	0.191	0.034	41	0.24	1000	platylobus 078
3	22								v. borealis 065
	23	0.07							v. borealis 067
	24	0.08	23	0.085	0.016	22	0.09		v. borealis 071
	43	0.08	23	0.088	0.003	22	0.09		v. borealis 126
	5	0.09	22	0.105	0.017	43	0.12		v. borealis 79027
	58	0.09	43	0.119	0.014	5	0.16		v. borealis Dorn 2158
	48	0.09	58	0.152	0.034	5	0.18		v. borealis 139
	44	0.08	48	0.127	-0.026	5	0.16	4	v. borealis 129
	LINK TO CLUSTER -1								
4	78								laetiflorus Peck 15248
	79	0.09							laetiflorus Heller 13670
	80	0.09	78	0.092	0.007	79	0.10		laetiflorus Cusick 1617
	81	0.09	78	0.110	0.018	80	0.14		laetiflorus Peck 15148
	74	0.12	80	0.148	0.038	81	0.18	4	laetiflorus Crum 1939

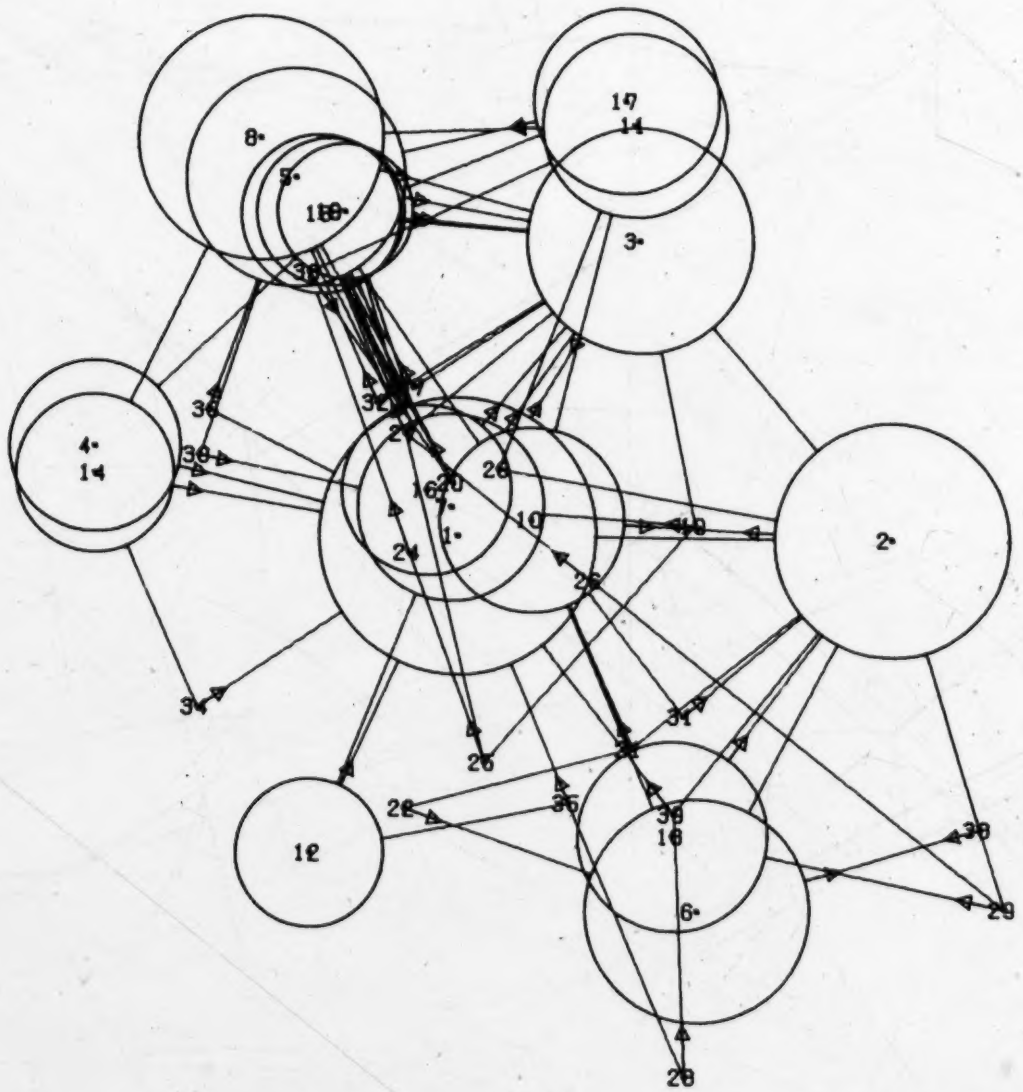
```
      LINK TO CLUSTER  -1
-------------------------------------------------------
 5   55                                          strept.   205
     57 0.09                                     strept.   207
      1 0.09    55 0.117 0.024   57 0.14        v. borealis    79001
     59 0.11    55 0.132 0.015   57 0.18        strept. Ost 5802

     48 0.10    59 0.157 0.026   57 0.21    4 v. borealis     139
      LINK TO CLUSTER  -3
-------------------------------------------------------
 6    7                                          multilobatus   021
     31 0.10                                     multilobatus   087
      9 0.11     7 0.124 0.024   31 0.14        multilobatus   024
     32 0.12     7 0.140 0.016    9 0.18        multilobatus   088

     61 0.15     7 0.185 0.046   32 0.23 1000 rubricaulis H.R.L. 2186
-------------------------------------------------------
 7   45                                          v. borealis    131
     47 0.11                                     v. borealis    138
      3 0.11    45 0.132 0.024   47 0.15        v. borealis    79012

     24 0.12    45 0.153 0.020    3 0.17    4 v. borealis     071
      LINK TO CLUSTER  -3
-------------------------------------------------------
 8   71                                          leonardi Weber 12145
     72 0.11                                     leonardi Schmoll 110
     73 0.11    72 0.127 0.018   71 0.14        leonardi Oster. 6712
     37 0.11    72 0.150 0.023   71 0.20        strept.   101A
     33 0.12    73 0.150-0.000   72 0.17        neomex. v. mutab.   093
     28 0.12    72 0.146-0.004   33 0.17        leonardi    080

      5 0.13    73 0.186 0.039   28 0.23 1004 v. borealis    79027
-------------------------------------------------------
 9   52                                          v. borealis    164
     53 0.11                                     v. borealis    173

     44 0.11    52 0.127 0.017   53 0.14    4 v. borealis     129
      LINK TO CLUSTER  -1
-------------------------------------------------------
10   29                                          rubricaulis   083
     30 0.11                                     rubricaulis   084
     26 0.12    30 0.134 0.024   29 0.15        platylobus    078

     64 0.12    26 0.141 0.006   29 0.17    4 platylobus Jeffery s.n.
      LINK TO CLUSTER  -2
-------------------------------------------------------
```

```
11   35                                                  leonardi     096
     38 0.12                                             leonardi     105
     70 0.12    38 0.135 0.017   35 0.15                 leonardi Mosquin & G

     72 0.13    38 0.146 0.011   35 0.17     4 leonardi Schmoll 110
      LINK TO CLUSTER  -8
-------------------------------------------------------
12   67                                                  suksdorfii Peck 17943
     68 0.12                                             suksdorfii Ownbeys 1842

     83 0.13    67 0.136 0.017   68 0.14     4 suksdorfii Peck 18055
      LINK TO CLUSTER  -1
-------------------------------------------------------
13    6                                                  v. borealis     79031
     16 0.12                                             v. borealis     054

     22 0.12    16 0.125 0.005    6 0.13     4 v. borealis     065
      LINK TO CLUSTER  -3
-------------------------------------------------------
14   49                                                  v. borealis 4X 152B
     50 0.13                                             v. borealis 4X 153

     74 0.13    50 0.165 0.038   49 0.20 1004 laetiflorus Crum 1939
-------------------------------------------------------
15    4                                                  v. borealis     79016
     46 0.13                                             v. borealis     137

     16 0.13     4 0.159 0.031   46 0.19 1004 v. borealis     054
-------------------------------------------------------
16   42                                                  strept.    109
     75 0.14                                             laetiflorus Heller 13670

      3 0.14    42 0.168 0.032   75 0.19 1004 v. borealis     79012
-------------------------------------------------------
17   15                                                  v. borealis     053
     21 0.15                                             strept.    061
.GT. FOUND FOR NEXT OTU **

     44 0.15    15 0.328 0.178   12 0.50 1004 v. borealis     129
-------------------------------------------------------
18   39                                                  strept. 106
     63 0.15                                             platylobus Maguire 13832
.GT. FOUND FOR NEXT OTU **

     64 0.15    39 0.328 0.176   14 0.50 1004 platylobus Jeffery s.n.
-------------------------------------------------------
```

ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)

CLUSTER	OTU	LABEL
19	2	v. borealis 79003
20	8	neomex. v. mutab. 022
21	10	multilobatus 025
22	11	multilobatus 027
23	12	laetiflorus 040
24	13	canus 047
25	14	canus 050
26	17	pauperculus 056
27	18	v. borealis 057
28	19	pauperculus 058
29	20	pauperculus 059
30	25	strept. 075
31	27	platylobus 079
32	34	neomex. v. mutab. 094
33	36	fendleri 101
34	51	v. borealis 4X 154
35	54	suksdorfii 199
36	56	strept. 206
37	60	strept. Holmgren 50
38	61	rubricaulis H.R.L. 2186
39	76	laetiflorus Heller 8076

Figure 2. Taxometric map of Analysis #1 (combined flavonoid and structural characters



THE SENECIO STREPTANTHIFOLIUS COMPLEX
SCALE: 1.83 CM = 100 UNITS

umbelliform capitulescence.

Clusters #16 and #17 are two-member clusters which are related to both the Cluster #3 complex and Cluster #5.

Cluster #18 is another two-member cluster related to Clusters #2 and #10 by its dissected leaves.

The taxometric map of the analysis is difficult to interpret because of the large number of clusters and adjoining lines superimposed on one another. For this reason, another map was hand-drawn so that only clusters #1-18 (those with >1 OTU), were plotted and only their nearest-neighbour distances shown (see Figure 3). From this latter map it is apparent that there are two major clusters, #1 and #3, each of which is the other's nearest neighbour. Of the remaining sixteen clusters only six do not have one of these two major clusters as their nearest neighbour.

Based upon these nearest neighbour relationships, the clusters themselves form two major groups, the cores of which are clusters #1 and #3 respectively.

As nearest neighbours to one another, clusters #1 and #3 form a link between the major groups but the groups themselves remain distinct. These two **groups** are labelled **A** and **B** in Figure 3.

In addition to the two major groups, two smaller groups were also defined on the basis of nearest neighbour relationships. Clusters #10 and #18 both have cluster #2 as their nearest neighbour. All three contain specimens with dissected leaves and are united as **group C** in Figure 3.

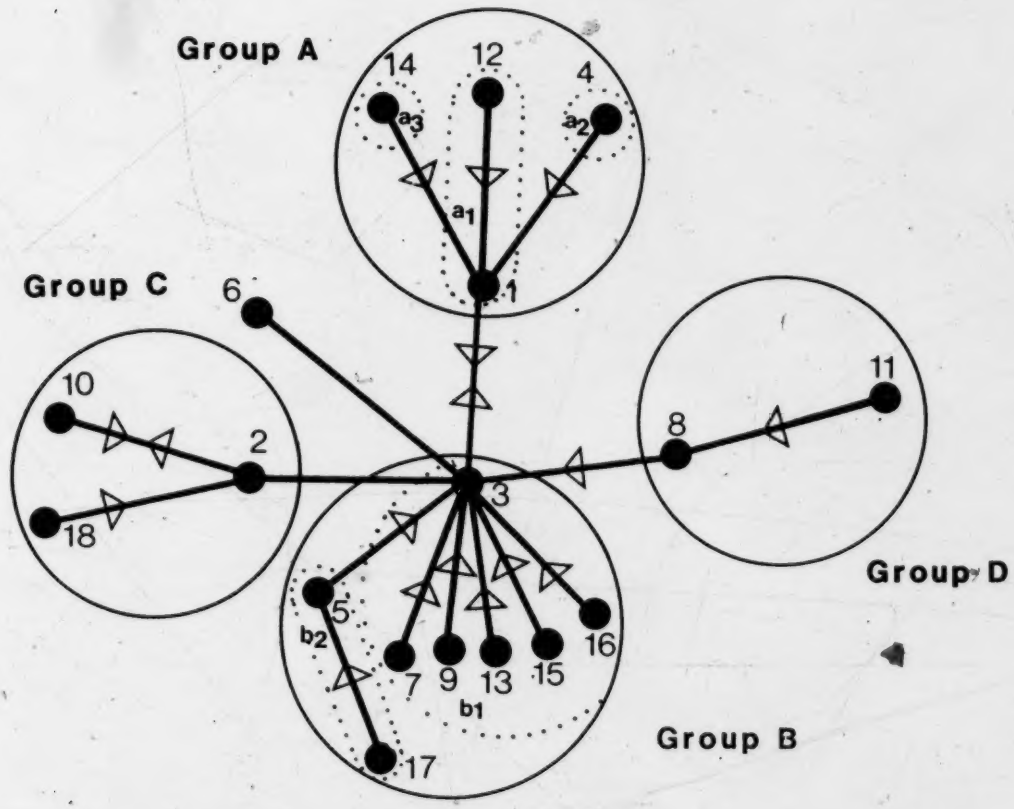
The nearest neighbour of cluster #11 is cluster #8. As previously mentioned, these clusters can be grouped together because both are composed of tomentose specimens. These two clusters comprise **group D**.

The relationships of the final two clusters are as follows:

i. The nearest neighbour of cluster #17 is cluster #5, which, in turn, is closely related to the central cluster, #3. For this reason cluster #17 is included in group B.

ii. Cluster #6 is distinct from the other clusters in **not** having one of

Figure 3. Nearest neighbour diagram of Analysis #1 (structural and flavonoid characters)



-- **black dots** represent OTU clusters (equivalent to the large open circles of Fig. 2)
-- **arrows** indicate nearest neighbours
-- **open circles** and **dotted lines** enclose the groups and sub-groups described in the text

them as a nearest neighbour.

All of the specimens in cluster #6 were previously identified as *S. multilobatus* and as such are not part of the *S. streptanthifolius* complex. Since #6 is the only cluster, (excluding single OTU clusters), which contains no specimen from the *S. streptanthifolius* complex, it is not surprising that its relationship is the most distant.

If we compare this analysis with the second analysis where only structural characters were used, (see Table 5; Figure 4) we see that, although the nearest neighbour diagrams look quite different, the essential relationships are the same. In general, those specimens that in the first analysis were placed in group B, (clusters #3,7,9,13,15), are found now in clusters #2,6,7. Those in group A, (clusters #1,4,12,14), are found in clusters #3,8,12. The tomentose specimens, formerly of group D, (cluster #8 and #11), are now in cluster #5, (and in related single OTU clusters #28,30,33). The specimens with moderately dissected leaves, group C, still cluster together in a major grouping, (#1,10,11,13), but are joined by a few specimens with more entire leaves. The *S. multilobatus* specimens, (cluster #4), are still on the periphery.

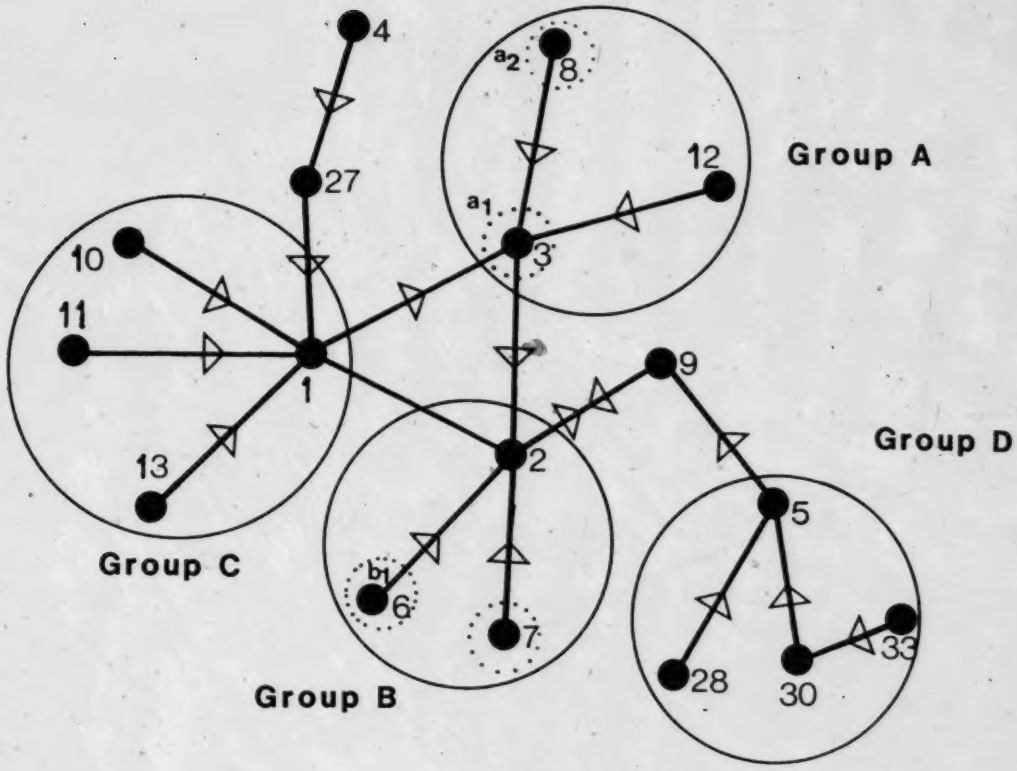
In both analyses, the apparent relationship of the clusters in group A is misleading. Ecological and distributional data, which were not included in the numerical analyses, are important in distinguishing some of the clusters. The specimens of cluster #4 in the first analysis, (#8 in the second), are generally found in damp alkali meadows in eastern Oregon and northern California, while those in cluster #14 of the first analysis, (members of #11 and #12 in the second), are from disturbed sites in the southwestern Yukon. Clusters #1 and #12 from the first analysis are united in the second analysis to form cluster #3. Distributional and ecological data support this merging. Based on this supplementary information, group A (analysis #1), can be easily divided into three distinct subgroups:

i. A_1, cluster #1 and #12

ii. A_2, cluster #4

iii. A_3, cluster #14.

Figure 4. Nearest neighbour diagram of Analysis #2 (structural and flavonoid characters)



-- **black dots** represent OTU clusters (equivalent to the large open circles of Fig. 2)
-- **arrows** indicate nearest neighbours
-- **open circles** and **dotted lines** enclose the groups and sub-groups described in the text

Table 5. Taxmap showing cluster membership for Analysis #2.

MAP CLUSTER ANALYSIS:-THE SENECIO STREPTANTHIFOLIUS COMPLEX -STRUCTURAL CHARACTERS ONLY

(MINIMUM NUCLEUS 0.157, MAXIMUM DROP 0.0226 BOTH ARE 100% OF NORMAL)
EQUALLY WEIGHTED ATTRIBUTES

CLUSTER NO.	OTU NOS	DIST BEST LINK	OTU BEST LINK	AVGOF NEW LINKS	DROP IN AVG.	FAR OTU	DIST FAR OTU	FLAG	TAXON & COLLECTOR
1	40								acutidens 107
	64	0.07							platyobus Jeffery s.n.
	66	0.07	40	0.082	0.015	64	0.09		acutidens Lingenfelter 73
	30	0.10	40	0.123	0.041	66	0.14		rubricaulis 084
	62	0.11	64	0.126	0.002	30	0.17		rubricaulis Cronq & D 2115
	65	0.12	40	0.144	0.018	30	0.18		acutidens Williams 1758
	41	0.12	62	0.161	0.018	66	0.19		acutidens 108
	26	0.12	64	0.173	0.011	65	0.23		platyobus 078
	57	0.12	64	0.149	-0.024	26	0.19		strept. 207
	46	0.12	57	0.174	0.025	26	0.24	1000	v. borealis 137
2	44								v. borealis 129
	48	0.08							v. borealis 139
	58	0.09	48	0.096	0.020	44	0.10		v. borealis Dorn 2158
	52	0.09	48	0.109	0.013	58	0.12		v. borealis 164
	43	0.09	58	0.110	0.001	44	0.13		v. borealis 126
	16	0.10	48	0.117	0.008	43	0.14		v. borealis 054
	23	0.10	16	0.119	0.002	44	0.14		v. borealis 067
	22	0.09	23	0.112	-0.007	48	0.13		v. borealis 065
	6	0.10	23	0.125	0.013	58	0.14		v. borealis 79031
	56	0.10	48	0.144	0.018	23	0.19		strept. 206
	82	0.10	56	0.137	-0.007	6	0.18		strept. Kruckeberg 55
	59	0.10	48	0.129	-0.007	82	0.15		strept. Ost 5802
	55	0.10	48	0.125	-0.004	82	0.16		strept. 205
	1	0.09	55	0.129	0.003	52	0.17		v. borealis 79001
	42	0.10	58	0.139	0.011	82	0.18		strept. 109
	24	0.11	23	0.146	0.007	56	0.19		v. borealis 071
	37	0.10	24	0.177	0.031	56	0.21	1000	strept. 101A
3	83								suksdorfii Peck 18055
	84	0.08							suksdorfii Williams 78-248
	85	0.09	84	0.119	0.034	83	0.14		suksdorfii Peck 18038
	69	0.10	83	0.125	0.006	85	0.17		suksdorfii Heller 9896
	77	0.10	84	0.142	0.017	69	0.18		laetiflorus UC 335863
	51	0.10	85	0.155	0.013	83	0.19		v. borealis 4X 154

```
      74 0.10   77 0.169 0.014  51 0.20       laetiflorus Crum 1939
      67 0.12   69 0.155-0.014  74 0.20       suksdorfii Peck 17943
      68 0.12   69 0.155 0.000  74 0.21       suksdorfii Ownbeys 1842

      82 0.11   68 0.148-0.008  74 0.19    4 strept. Kruckeberg 55
       LINK TO CLUSTER  -2
-------------------------------------------------------
 4    7                                      multilobatus   021
      9 0.11                                 multilobatus   024
     31 0.14    7 0.139 0.032   9 0.14       multilobatus    087

     81 0.15    7 0.170 0.031  31 0.19 1000 rubricaulis H.R.L. 2186
-------------------------------------------------------
 5   71                                      leonardi Weber 12145
     72 0.11                                 leonardi Schmoll 110
     73 0.11   72 0.127 0.018  71 0.14       leonardi Oster 6712
     33 0.12   73 0.136 0.009  71 0.16       neomex. v. mutab.    093

      5 0.13   73 0.166 0.030  71 0.19 1000 v. borealis 79027
-------------------------------------------------------
 6    3                                      v. borealis 79012
     45 0.11                                 v. borealis 131
     47 0.12   45 0.134 0.020   3 0.15       v. borealis 138
      2 0.12   45 0.138 0.004   3 0.15       v. borealis 79003

     48 0.12    3 0.158 0.020  47 0.19    4 v. borealis 139
       LINK TO CLUSTER  -2
-------------------------------------------------------
 7   15                                      v. borealis 053
     53 0.12                                 v. borealis 173

     22 0.12   53 0.120 0.003  15 0.12    4 v. borealis 065
       LINK TO CLUSTER  -2
-------------------------------------------------------
 8   78                                      laetiflorus Peck 15248
     79 0.12                                 laetiflorus Heller 13670
     80 0.12   78 0.128 0.008  79 0.14       laetiflorus Cusick 1617

     74 0.12   80 0.136 0.008  79 0.14    4 laetiflorus Crum 1939
       LINK TO CLUSTER  -3
-------------------------------------------------------
 9   34                                      neomex. v. mutab.    094
     37 0.12                                 strept.    101A

     33 0.13   37 0.154 0.030  34 0.18    4 neomex. v. mutab.    093
       LINK TO CLUSTER  -5
```

```
-------------------------------------------------------
 10   21                                        strept.   061
      46 0.13                                   v. borealis 137
 .GT. FOUND FOR NEXT OTU **

      62 0.13   21 0.314 0.188   14 0.50 1004 rubricaulis Cronq & D 2115
-------------------------------------------------------
 11   25                                        strept.   075
      27 0.13                                   platyobus 079
      28 0.13   27 0.153 0.024   25 0.17       leonardi  080
      49 0.13   28 0.159 0.007   25 0.19       v. borealis 4X 152B

      59 0.13   27 0.161 0.002   25 0.17    4 strept. Ost 5802
       LINK TO CLUSTER  -2
-------------------------------------------------------
 12   50                                        v. borealis 4X 153
      61 0.15                                   rubricaulis H.R.L. 2186
 .GT. FOUND FOR NEXT OTU **

      30 0.15   61 0.325 0.175   14 0.50 1004 rubricaulis    084
-------------------------------------------------------
 13   39                                        strept. 106
      63 0.15                                   platyobus Maguire 13832
 .GT. FOUND FOR NEXT OTU **

      64 0.15   39 0.326 0.174   14 0.50 1004 platyobus Jeffery s.n.
-------------------------------------------------------
ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)

CLUSTER OTU LABEL
     14   4 v. boraelis    79016
     15   5 v. borealis    79027
     16   8 neomex. v. mutab   022
     17  10 multilobatus  025
     18  11 multilobatus   027
     19  12 laetiflorus    040
     20  13 canus   047
     21  14 canus  050
     22  17 pauperculus   056
     23  18 v. borealis   057
     24  19 pauperculus   058
     25  20 pauperculus   059
     26  29 rubricaulis    083
     27  32 multilobatus    088
     28  35 leonardi    096
     29  36 fendleri  101
```

30 38 leonardi 105
31 54 suksdorfii . 199
32 60 strept. Holmgren 50
33 70 leonardi Mosquin & G
34 75 laetiflorus Heller 13670
35 76 laetiflorus Heller 8076
36 81 laetiflorus Peck 15148

Using the same approach, cluster #5 (analysis #1) can be separated from the rest of group B by the more southern distribution of its specimens. Based upon this fact and its smaller leaf length/width ratios, cluster #5 is considered as distinct from the rest of group B. Cluster #17 is also grouped separately with cluster #5 because #5 is its nearest neighbour. These two clusters make up sub-group B_2. The rest of group B will be referred to as sub-group B_1.

Both numerical analyses are in agreement then in dividing the *S. streptanthifolius* complex taxa into four large groups. Furthermore, in each analysis, what was identified as group A further subdivided into three sub-groups after the inclusion of ecological and distributional data. Finally, in analysis #1, a sub-group of group B was identified using distributional data and nearest neighbour data. Therefore group B was split into sub-groups B_1 and B_2. Thus the *S. streptanthifolius* complex is divided into seven groups or taxa.

In an attempt to ascertain the correct name for each of the seven taxa, a third numerical analysis was undertaken. For this analysis, twelve type specimens were included in the OTU set. Only a limited amount of data could be gathered from each type specimen without harming it; therefore the relationships between the types as expressed in the third analysis were derived from a very reduced number of characters. Not only will this give a less precise indication of the relationship, it will in some cases alter the previously apparent relationships of other OTUs in the analysis since the measured discontinuities are relative. Thus the changes in relationships that appear in analysis #3 represent small reductions in the precision of measurement, brought about by the incomplete data set used for the type specimens. Therefore, since it is less reliable, the interpretation of analysis #3 must be made with reference to the two previous analyses. The results are presented in Table 6.

Cluster #1, which is analogous to group C from the previous analyses, includes two type specimens, *S. rubricaulis* and *S. platylobus*. Of the two names, *Senecio rubricaulis* has priority so it is adopted. Group C is now called *S. streptanthifolius* var. *rubricaulis*. Justification for using the name at the varietal level follows in a later section.

Table 6. Taxmap showing cluster membership for Analysis #3 (including type specimens)

MAP CLUSTER ANALYSIS:-THE SENECIO STREPTANTHIFOLIUS COMPLEX - TYPE SPECIMENS INCLUDED

(MINIMUM NUCLEUS 0.153; MAXIMUM DROP 0.0226 BOTH ARE 100% OF NORMAL)
EQUALLY WEIGHTED ATTRIBUTES

CLUSTER NO.	OTU NOS	DIST BEST LINK	OTU BEST LINK	AVGOF NEW LINKS	DROP IN AVG.	FAR OTU	DIST FAR OTU	FLAG	TAXON & COLLECTOR
1	40								acutidens 107
	64	0.06							platylobus Jeffery s.n.
	66	0.07	40	0.080	0.015	64	0.09		acutidens Lingenfelter 73
	30	0.10	40	0.121	0.042	66	0.14		rubricaulis 084
	62	0.10	64	0.123	0.001	30	0.16		rubricaulis Cronq & D 2115
	41	0.12	62	0.151	0.029	66	0.18		acutidens 108
	65	0.12	40	0.149	-0.003	41	0.18		acutidens Williams 1758
	26	0.12	64	0.168	0.019	65	0.22		platylobus 078
	87	0.12	62	0.140	-0.028	26	0.19		TYPE platylobus
	88	0.08	87	0.135	-0.005	26	0.19		TYPE rubricaulis
	84	0.11	88	0.174	0.039	26	0.23	1000	TYPE suksdorfii
2	44								v. borealis 129
	48	0.07							v. borealis 139
	58	0.09	48	0.093	0.018	44	0.10		v. borealis Dorn 2158
	52	0.09	48	0.106	0.013	58	0.12		v. borealis 164
	80	0.09	48	0.117	0.011	44	0.14		TYPE aquariensis
	43	0.09	58	0.113	-0.004	80	0.14		v. borealis 126
	16	0.09	48	0.120	0.007	80	0.15		v. borealis 054
	23	0.09	16	0.116	-0.004	44	0.14		v. borealis 067
	22	0.09	23	0.113	-0.003	80	0.14		v. borealis 065
	6	0.10	23	0.125	0.013	80	0.15		v. borealis 79031
	3	0.10	80	0.134	0.009	43	0.15		v. borealis 79012
	56	0.10	48	0.139	0.005	23	0.18		strept. 206
	94	0.10	56	0.133	-0.006	6	0.18		strept. Kruckeberg 5501
	59	0.10	48	0.125	-0.008	94	0.14		strept. Osterhout 5802
	55	0.10	48	0.125	0.000	94	0.16		strept. 205
	1	0.09	55	0.129	0.004	52	0.17		v. borealis 79001
	85	0.10	59	0.142	0.012	52	0.18		TYPE cymbalarioides
	84	0.09	85	0.141	-0.001	22	0.18		TYPE suksdorfii
	42	0.10	58	0.142	0.001	94	0.17		strept. 109
	4	0.10	44	0.144	0.002	23	0.18		v. borealis 79016
	60	0.10	1	0.164	0.020	80	0.22		strept. Holmgren 50
	24	0.10	23	0.153	-0.011	84	0.20		v. borealis 071
	37	0.10	24	0.185	0.032	84	0.24	1000	strept. 101A

```
-------------------------------------------------------
 3   95                                          suksdorfii Peck 18055
     96 0.08                                     suksdorfii Williams 78-248
     97 0.09   96 0.115 0.032  95 0.14           suksdorfii Peck 18038
     69 0.09   95 0.121 0.006  97 0.16           suksdorfii Heller 9896
     77 0.09   96 0.138 0.017  69 0.17           laetiflorus UC 335863

     78 0.10   97 0.162 0.024  69 0.23 1000 TYPE str
-------------------------------------------------------
 4    7                                          multilobatus   021
      9 0.10                                     multilobatus   024
     31 0.14    7 0.137 0.032   9 0.14           multilobatus    087

     61 0.14    7 0.165 0.028  31 0.18 1000 rubricaulis H.R.L. 2186
-------------------------------------------------------
 5   71                                          leonardi Weber 12145
     72 0.11                                     leonardi Schmoll 110
     73 0.11   72 0.126 0.019  71 0.14           leonardi Oster 6712
     33 0.11   73 0.134 0.009  71 0.16           neomex. v. mutab.  093

      5 0.12   73 0.164 0.030  71 0.19 1000 v. borealis    79027
-------------------------------------------------------
 6   46                                          v. borealis    137
     57 0.11                                     strept.   207
     51 0.12   57 0.135 0.021  46 0.15           v. borealis 4X 154
     78 0.12   51 0.142 0.007  46 0.16           TYPE strept.

     87 0.12   51 0.138-0.004  46 0.16    4 TYPE platylobus
      LINK TO CLUSTER  -1
-------------------------------------------------------
 7   45                                          v. borealis    131
     47 0.11                                     v. borealis    138
      2 0.12   45 0.131 0.017  47 0.14           v. borealis    79003

     22 0.13   45 0.155 0.024  47 0.18 1004 v. borealis    065
-------------------------------------------------------
 8   67                                          suksdorfii Peck 17943
     68 0.11                                     suksdorfii Ownbeys 1842
.GT. FOUND FOR NEXT OTU **

     69 0.12   68 0.321 0.206  11 0.53 1004 suksdorfii Heller 9896
-------------------------------------------------------
 9   15                                          v. borealis    053
     53 0.12                                     v. borealis    173

     22 0.12   53 0.119 0.003  15 0.12    4 v. borealis    065
```

```
      LINK TO CLUSTER  -2
-------------------------------------------------
 10   90                                    laetiflorus Peck 15248
      92 0.12                               laetiflorus Cusick 1617
      91 0.12   90 0.125 0.008  92 0.13     laetiflorus Heller 13670

      95 0.12   90 0.147 0.022  91 0.19   4 suksdorfii Peck 18055
       LINK TO CLUSTER  -3
-------------------------------------------------
 11   34                                    neomex. v. mutab. 094
      37 0.12                               strept.   101A

      33 0.13   37 0.152 0.029  34 0.18   4 neomex. v. mutab.  093
       LINK TO CLUSTER  -5
-------------------------------------------------
 12   25                                    strept.   075
      27 0.13                               platylobus   079
      28 0.13   27 0.150 0.023  25 0.17     leonardi    080
      49 0.13   28 0.156 0.006  25 0.18     v. borealis 4X 152B

      59 0.13   27 0.159 0.004  25 0.17   4 strept. Osterhout 5802
       LINK TO CLUSTER  -2
-------------------------------------------------
 13   21                                    strept.   061
      83 0.13                               TYPE dileptiifolius
 .GT. FOUND FOR NEXT OTU **

      62 0.13   83 0.327 0.199  14 0.53 1004 rubricaulis Cronq & D 2115
-------------------------------------------------
 14   50                                    v. borealis 4X 153
      74 0.13                               laetiflorus Crum 1939

      64 0.14   50 0.155 0.024  74 0.17 1004 platylobus Jeffery s.n.
-------------------------------------------------
 15   39                                    strept. 106
      63 0.15                               platylobus Maguire 13832
 .GT. FOUND FOR NEXT OTU **

      64 0.15   39 0.336 0.190  14 0.53 1004 platylobus Jeffery s.n.
-------------------------------------------------
ISOLATED OTU'S (SINGLE MEMBER CLUSTERS)

CLUSTER OTU LABEL
     16   5 v. borealis    79027
     17   8 neomex. v. mutab.   022
     18  10 rubricaulis  025
```

19 11 multilobatus 027
20 12 laetiflorus 040
21 13 canus 047
22 14 canus 050
23 17 pauperculus 056
24 18 v. borealis 057
25 19 pauperculus 058
26 20 pauperculus 059
27 29 rubricaulis 083
28 32 multilobatus 088
29 35 leonardi 096
30 36 fendleri 101
31 38 leonardi 105
32 54 suksdorfii 199
33 61 rubricaulis H.R.L. 2186
34 70 leonardi Mosquin & Gillett
35 75 laetiflorus Heller 13670
36 76 laetiflorus Heller 8076
37 79 TYPE ward
38 81 TYPE pammellii
39 82 TYPE willingii
40 86 TYPE laetiflorus
41 89 TYPE farriae
42 93 laetiflorus Peck 15148

Clusters #2,6,7,8,13 all fall into group B as delineated in the first analysis. A total of five types are included in these clusters. Of the five, the oldest name is *S. streptanthifolius*. The sub-groups B_1 and B_2, identified from analysis #1, are not apparent in this analysis, however, the collection locality and small leaf length/width ratios of the *S. streptanthifolius* type specimen very clearly place it in the smaller, more southern sub-group B_2. For this reason, sub-group B_2 is now called *S. streptanthifolius*.

The northern sub-group, although mixed with southern specimens in the large cluster #2 is represented exclusively in cluster #7. This sub-group has been recognized before as *S. cymbalarioides* Nutt. var. *borealis* by Greenman (1916). Although Greenman did not specifically designate a type specimen, an examination of the specimens he cited clearly indicates that his view of var. *borealis* included the northern specimens, sub-group B_1, and excluded the southern ones, (var. *cymbalarioides* and var. *streptanthifolius* in his treatment). This large sub-group B_1 will hereafter be referred to as *S. streptanthifolius* var. *borealis*. The nomenclatural problems will be fully dealt with in the Taxonomy section.

Four of the five remaining groups from the first analysis are also recognizable in this analysis; however, in no instance is a type specimen associated with any of them. In the case of group D, the type specimens of *S. oodes* Rydb. and *S. leonardii* Rydb. would be the most likely to cluster in that group because they are tomentose. However, these specimens, although examined visually, were not available for the analysis. *S. oodes* is chosen as the name for group D since it predates *S. leonardii*.

Of the remaining three groups, two have been recognized in the past by other researchers. Based on the original descriptions, the collection locality, and a visual examination of the type specimen of *S. laetiflorus*, it is apparent that *S. laetiflorus* is the appropriate name for sub-group A_2. The type specimen was included in the analysis; it separated, however, as a single unit cluster (#40). It is assumed that the reduced number of characters scored for the type is responsible for its not clustering with any other specimens.

In the case of sub-group A_1, the type previously associated with this entity, *S. suksdorfii*, clusters in a large group B cluster and is therefore part of *S. streptanthifolius*. Examination of *S. suksdorfii* and its collection locality supports this placement. Sub-group A_1 only includes specimens with leaves that are more ovate with truncate to cordate bases. Also they are generally smaller with fewer heads than those in group B. Flavonoid profiles are also important for defining sub-group A_1. Two specimens of *S. laetiflorus* are erroneously included in cluster #1 (Table 4) because no flavonoid data were available for them. In addition to flavonoid data, these two taxa are normally separable using ecological data however, as mentioned these were not included in the analysis either. The separation of the type means that sub-group A_1 now requires a name. It is here named *S. wallowensis*.

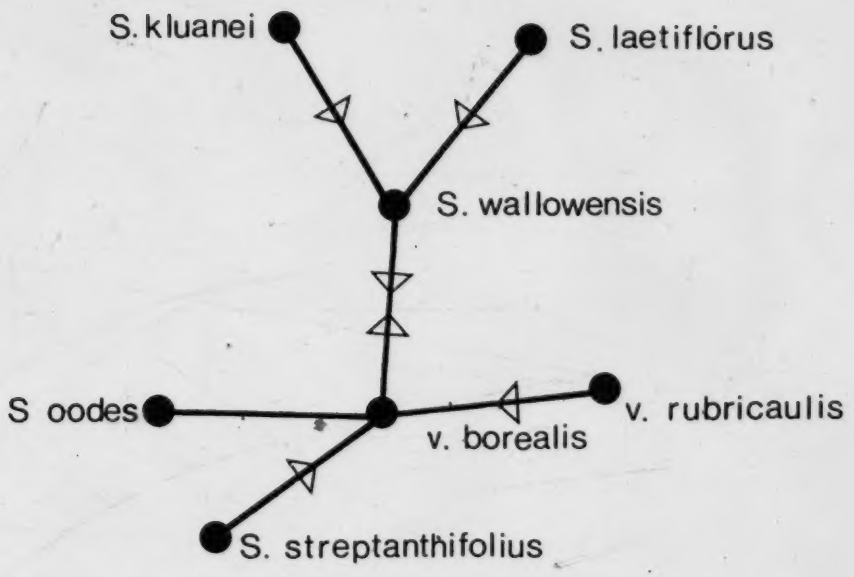
Sub-group A_3 has not been recognized in the past. It is here named *S. kluanei*. A formal taxonomic treatment of these last two taxa follows in the Taxonomy section. A summary of the seven taxa proposed appears in Table 7.

Statistical Analysis

The Kruskal-Wallis test (non-parametric analysis of variance) which was conducted using thirty-two structural characters and the seven taxa derived from the numerical analysis yielded the following results.

The characters were divided into three categories. For seven characters the H-statistic was not significant at the .05 level so the characters were not considered valid for separating taxa. Of the remaining twenty-five significant at the .05 level, sixteen were significant at better than the .005 level. It was from this third category that characters used to construct the dichotomous key (Taxonomy section) were chosen. All of the characters are presented in their respective categories in Table 8. Those of the more significant characters (category 3) which require some explanation are described below.

Table 7. Taxa recognized from the numerical analysis (diagram redrawn from Figure 3)



S. wallowensis	sub-group A_1
S. laetiflorus	sub-group A_2
S. kluanei	sub-group A_3
S. streptanthifolius var. *borealis*	sub-group B_1
S. streptanthifolius var. *streptanthifolius*	sub-group B_2
S. oodes	group C
S. streptanthifolius var. *rubricaulis*	group D

Table 8 Character categories resulting from the Kruskal-Wallis Test

characters not significant at .05 level	characters significant at >.05 level	characters significant at >.005 level
basal leaf apical margins	root type	stalk height
cauline leaf bases	cauline leaf number	leaf pubescence
stalk number	secondary stalk number	basal leaf lwr. margins
involucre width at base	upp. invol. pubescence	petiole length
pappus length	involucre length	cauline leaf margins
ray floret length	head diameter	head number
ray floret number	phyllary length	lwr. invol. pubescence
	phyllary number	disc floret length
	maximum leaf width	anther length
		disc floret number
		leaf perimeter
		leaf base
		width/distance ratio
		leaf length
		leaf perimeter ratio
		leaf length/width ratio

Leaf pubescence has always been an important character in aureoid taxonomy, having been used in the past to delimit the section *Tomentosi*. Leaf pubescence as it is used here, refers to tomentum on either or both sides of the actual leaf blade and does not include those instances where only the axils are tomentose. In no instance were leaves tomentose to the same degree as *S. canus*. Although *S. oodes* was the only *S. streptanthifolius* taxon where the leaves were always pubescent, other taxa exhibited this trait to a lesser degree.

Basal leaf lower margins was considered a separate character from apical leaf margins because a characteristic pattern of the aureoid complex, is to have entire margins at the base of the leaf but dentate or serrate margins at the tip. It was felt that this pattern was more easily portrayed when divided into two characters.

The aureoid complex has been characterized as having reduced **cauline leaves** (Barkley, 1978; Weber and Löve, 1981). These cauline leaves may, however, be categorized as highly dissected or alternatively, as mere bracts. Occasionally plants have highly reduced, bract-like lobate leaves. In these cases an intermediate value was scored.

The **involucre pubescence** is an easily observable character which appears to be less variable than leaf pubescence. Like the leaf margins character, this too has been treated as two characters (upper and lower involucre) so that the different areas of pubescence could be coded. Lower involucre pubescence was the more useful of the two characters.

The **number of heads** in an inflorescence was defined in this study such that heads borne on stalks originating below the highest cauline leaf were excluded since these stalks were considered to be secondary stalks bearing secondary capitulescences. Defined in this manner, head number ranged from its highest values in *S. streptanthifolius* var. *borealis* to its lowest values in *S. wallowensis*.

Anther length was measured from the tip to the bottom of the anther base. All measurements were made on dehisced anthers.

The final four characters were all measured by computer as discussed in the Methods section.

The **leaf perimeter** is a measure of overall leaf size and/or dissection. By contrast, the **leaf perimeter/polygon** ratio is a measure of the extent of leaf dissection and quantifies the amount of dissection with no reference to pattern. Since the perimeter of the polygon enclosing the leaf represents the shortest distance around the leaf, any deviation from entirety will increase the value of the ratio. As expected, var. *rubricaulis* showed the largest values.

The **basal leaf angle** is a measure of the shape of the leaf base; a measure of 180° indicates a truncate base, a higher value - cordate. *S. wallowensis* had the highest values, (the most truncate-cordate leaf base), while *S. kluanei* had the lowest.

The **leaf width/distance ratio** was calculated by dividing the distance from the leaf apex to the point of maximum width by the total leaf length.

The statistical analysis clearly demonstrates that the taxa are separable based on data provided by a variety of characters. Characters like anther length and leaf perimeter are difficult to measure and so may be of limited value to the field botanist, however many other characters such as disc floret length, disc floret number, and basal leaf angle provide reliable and accessible means by which taxa may be identified. The examination of the means and standard deviations of the characters presented (see appendix) also revealed that there is no instance where a single character is diagnostic for a taxon. A character is considered to be diagnostic if its mean value for a taxon ± one standard deviation does not overlap with that of any other taxon. The results therefore do not alleviate the necessity of using a number of characters when identifying taxa. Table 9 summarizes the sixteen characters used to separate the seven taxa.

Table 9. Comparative structural characters in the *S. streptanthifolius* complex

	S. streptanthifolius - varieties			other species in the complex			
	streptanth.	*borealis*	*rubricaulis*	*laetiflorus*	*wallowensis*	*oodes*	*kluanei*
stalk height (cm.)	*20-38 **28.0	22.5-47 29.6	26.3-64 41.7	28-62 43.0	8.5-36 17.2	15-43 31.9	14.5-30 24.5
leaf pubescence	glabrous	glabrous	glabrous	glabrous or lightly tomentose	glabrous	tomentose	glabrous or lightly tomentose
lower leaf margins	entire	entire	dentate-lobate	entire or lobate	entire to crenate-serrate	serrate to dentate-serrate	deeply serrate to dentate-serrate
petiole length (cm.)	2.1-5.0 4.0	2.0-8.5 3.7	1.8-9.5 5.6	5.3-11.0 7.9	1.7-5.0 2.8	2.2-9.0 4.6	2.2-4.0 3.1
cauline leaf margins	entire or seldom dissected	entire	dissected	dissected	entire or dissected	entire or seldom dissected	entire or seldom dissected
[1]lwr. invol. pubescence	glabrous	glabrous or rarely tomentose	glabrous	glabrous or rarely tomentose	glabrous	densely tomentose	tomentose
head number	5-20 12.5	3-35 14.1	7-20 13.8	8-12 9.8	3-9 5.7	5-11 8.5	5-14 8.7
disc floret number	21-45 33.7	25-54 36.2	25-43 32.7	45-96 64.7	39-72 57.9	22-63 40.8	39-58 46.0
disc length (mm.)	5.3-6.4 5.8	4.0-6.5 5.7	5.5-8.0 6.5	3.5-5.5 4.8	4.2-6.0 5.1	5.2-6.5 6.0	5.8-6.2 6.0
anther length (mm.)	2.2-3.0 2.7	1.8-2.8 2.3	2.2-3.2 2.9	1.8-2.5 2.2	2.0-2.5 2.2	2.0-3.0 2.5	2.5-2.8 2.6

leaf perimeter (cm.)	4.1–12.9 7.52	4.9–11.3 7.20	6.7–19.6 12.5	6.3–21.2 11.8	3.3–9.7 5.4	4.1–14.0 9.7	8.8–19.8 12.7
[2]leaf perimeter ratio	1.0–1.2 1.09	1.0–1.1 1.05	1.1–1.9 1.38	1.0–1.6 1.22	1.0–1.2 1.08	1.0–1.4 1.20	1.0–1.3 1.21
basal leaf angle (°)	18.0–62.0 35.7	7.0–91.0 31.3	13.0–142.0 60.5	27.0–58.0 45.6	31.0–143.0 87.0	5.0–56.0 33.1	9.0–31.0 19.0
leaf length (cm.)	1.8–4.8 2.92	1.9–4.7 2.99	2.5–4.5 3.47	3.2–10.8 5.07	1.0–4.4 1.85	1.7–4.0 3.28	2.4–3.1 2.89
[3]width/distance ratio	0.23–0.45 0.37	0.03–0.49 0.32	0.35–0.66 0.44	0.43–0.53 0.48	0.37–0.56 0.48	0.33–0.55 0.43	0.33–0.57 0.45
length/width ratio	1.6–2.4 2.0	1.2–3.6 2.6	1.3–3.0 1.8	1.5–4.3 2.6	0.8–2.9 1.3	1.3–2.5 2.0	2.4–2.5 2.4

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*range values
**mean values
[1]lwr. invol. = lower involucre
[2]leaf perimeter ratio = ratio of leaf perimeter to outer polygon perimeter – larger values indicate greater leaf dissection
[3]width/distance ratio = ratio of distance between leaf apex and point of maximum leaf width to total leaf length.

B. Chromosome Numbers

A total of 75 counts have been made from aureoid senecios within and related to the *S. streptanthifolius* complex, the results of which are presented in Table 10. A photograph of meiotic chromosome configurations in the aureoid complex appears in Figure 5. The fact that the 75 new counts presented are all multiples of 23 strongly supports the idea that x=23 is indeed the base chromosome number for the aureoid complex. Furthermore, in no case was there convincing evidence for the existence of any aneuploid populations within the study area. Although some difficulty was encountered in counting, it was found that in most cases through persistence and reliance on multiple counts for verification, that a chromosome number of 23 or a multiple of same was achieved for each population. Although the possible existence of aneuploid individuals cannot be disproven by this method, the present study shows that they are not common and apparently are not of major importance in aureoid senecio populations examined.

With the exception of lagging chromosomes no meiotic irregularities were apparent in any of the preparations. Lagging chromosomes, however, were quite common. Numerous tests of pollen viability in conjunction with this anomaly were carried out and in all cases pollen from the same population was apparently completely viable. Lagging chromosomes therefore, are not considered a critical problem to meiosis within the group. The apparent lack of complication in meiosis is expected from a successfully outcrossing complex such as this.

Two ploidy levels are reported for the *Senecio streptanthifolius* complex: a diploid, (n=23), and a tetraploid, (n=46). The existence of tetraploid populations within the species has been reported only once before (Morton, 1981) although allusion to their possible existence has been made in the past (Barkley, 1962). The new reports presented here help to define the ranges of the two chromosome races as well as supplying much needed information on the chromosome numbers of the various phases. Data from the

Table 10. New chromosome counts in the *S. streptanthifolius* complex and related species

TAXON	n	LOCATION	*COLL. NO.
S. canus	46	ALTA.: Waterton Lakes Nat'l. Pk.	192
	2n=138	ALTA.: Cardinal River Valley	79033
	46	ALTA.: roadbank by Cataract Creek, Kananaskis Hwy.	79025
	69	B.C.: between Cranbrook and Ft. Steele	050
	46	CA.: 12 km. N. of Weed on Hwy. 97	041
	46	OR.: Nat'l. Forest Rd#39 S. of Joseph, 6.4 km. N. of Lick Creek	193
	23	OR.: along Hwy 199, ca. 4.8 mi. N. of Obrien	039
	46	OR.: 64 km. E. of Klamath Falls	038
	23	OR.: 45 km W. of John Day	048
	23	OR.: ca. 16 km. N. of Burns on #395	047
S. fendleri	23	CO.: 8 km W. of summit of Monarch Pass on roadside, Hwy 50	101
S. indecorus	92	YUKON: Skagway Hwy., 6.1 km S. of Carcross bridge	79002
	88-92	YUKON: km 100.4, S. Canol Road	79014
S. kluanei	46	YUKON: 1 km. E. of Haines Jctn on Hwy #1 (Alaska Hwy)	152B
	46	YUKON: km. 1538 - Alaska Hwy, W. of Whitehorse	153
	46	YUKON: Lake Labarge	154
S. laetiflorus	23	CA.: 3.2 km. S. of Gazelle	040
S. multilobatus	46	AZ.: along trail from Pioneer Pass to Pinal Peak, Pinal Mtns.	013

	46	AZ.: approx. 4 km. south of Pioneer Pass	015
	ca. 23	CO.: roadside S. of Jctn. of C-141 & C-145	021
	46	NV.: west side of Ruby Lake	029
	23	NV.: along Hwy 93, ca. 90 km. S. of Ely	027
	46	NM.: on Burro Mtn. south of Silver City	007
	46	UT.: along road to Panaca, Nevada	026
	23	UT.: Hwy 95, ca. 5km W. of jctn. with Rte 163	024
S. neomexicanus var. *metcalfei*	46	NM.: 20 km. N. of Silver City	005
	46	NM.: Hwy#90 - 16 km. W. of Kingston	003
S. neomexicanus var. *mutabilis*	23	UT.: 2 km W. of Monticello	022
	23	CO.: W. of Silverton on Hwy#550	093
	23	CO.: Plumtaw Rd., NW of Pagosa Springs	094
S. neomexicanus var. *neomexicanus*	23	AZ.: 12.8 km. S. of Showlow	010
	23	NM.: along Hwy#90, 0.4 km. W. of Emory Pass	001
	23	NM.: 3 km below Saliz Pass on Hwy#180 between Alma and Reserve	008
S. neomexicanus var. *toumeyi*	23	AZ.: Pinal Mtns, S. of Globe along road to Pioneer Pass	012
S. oodes	23	CO.: 7 km E. of Red Cliff	105
	23	CO.: E. side of Wolf Creek Pass	096
	23	CO.: E. side of Wolf Creek Pass	096A
	23	WY.: 2.5 km W. of Bear River	080

S. pauperculus	46	ALTA.: 30 km N. of Whitecourt along Hwy#43	062
	ca. 23	ALTA.: Banff National Park, Eisenhower Jctn.	79021
	46	ALTA.: Kananaskis Lake at south end of Lower Lake	79022
	46	ALTA.: Kananaskis Hwy, mile 90-95, ca. 64 km. N. of Cataract Creek	79023
	46	B.C.: 20 km. S. of Savona	056
	46	B.C.: ca. 18 km. S. of Savona	059
	23	B.C.: km 775 - Hwy 97 (Alaska Hwy)	165
	23	B.C.: km 696-Alaska Hwy.	168
	ca. 46	NWT: 10 km. S. of Hay River	063
	46	NWT: 20 km S. of Enterprise	064
	46	NWT: km. 116 - Hwy#1, 32 km. W. of Enterprise	070
S. pseudaureus var. *flavulus*	23	ID.: E. of Leslie, SE of Mackay	76
S. streptanthifolius var. *borealis*	23	B.C.: 20 km. S. of Savona	054
	46	B.C.: 20 km. S. of Savona near streambank	057
	23	B.C.: roadside between 70 Mile House and Green Lake Park	061
	23	B.C.: ca. 40 km. W. of Dease Lake on road to Telegraph Creek	126
	23	B.C.: ca. 12.8 km. N. of Dease Lake along Hwy #37(Cassian Hwy.)	131
	23	B.C.: ca. 64 km. N. of Atlin	137
	23	B.C.: 35.2 km. S. of Watson Lake	164
	23	YUKON: between Tagish & Jake's Corners	138

	23	YUKON: 3.2 km. N. of Carcross	139
	23	YUKON: km. 150, Skagway-Whitehorse Road	79001
S. streptanthifolius var. *rubricaulis*	46	UT.: vicinity of Naomi Pk.	078
	46	UT.: above Bear Lake, W. of Garden City	079
	23	UT.: ca. 2 km E. of Elizabeth Pass	083
	23	UT.: 12 km. W. of Elizabeth Pass	084
	23	UT.: S. of Lilly Lake & Lost Lake	085
	46	WY.: 14.5 km. N. of Hwy 187-189, N. of Bondurant	106
	46	WY.: 16 km. W. of Hwy.187-189 on Hwy#22 toward Teton Pass	107
	23	WY.: ca. 10km. N. of Moran	108
S. streptanthifolius var.*streptanthifolius*	23	CA.: Sonora Pass - Sweetwater Mtns.	206
	2n=46	CO.: 8.3 km W. of summit of Monarch Pass	101A
	23	MT.: 3.3 km S. of Cascade Co. line at King's Hill Pass	109
	23	WA.: Wanatchee Mtns.- Iron Creek Trail, ca. 16 km. NNE of Cle Elum	205
S. streptanthifolius X pauperculus	46	ID.: ca. 11.2 km. SE. of Baker	075
S. tridenticulatus	23	CO.: N. side of Spring Creek Pass	098
S. wallowensis	23	OR.: Ice Lake, Wallowa Mtns.	199

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* all collections were made by the author

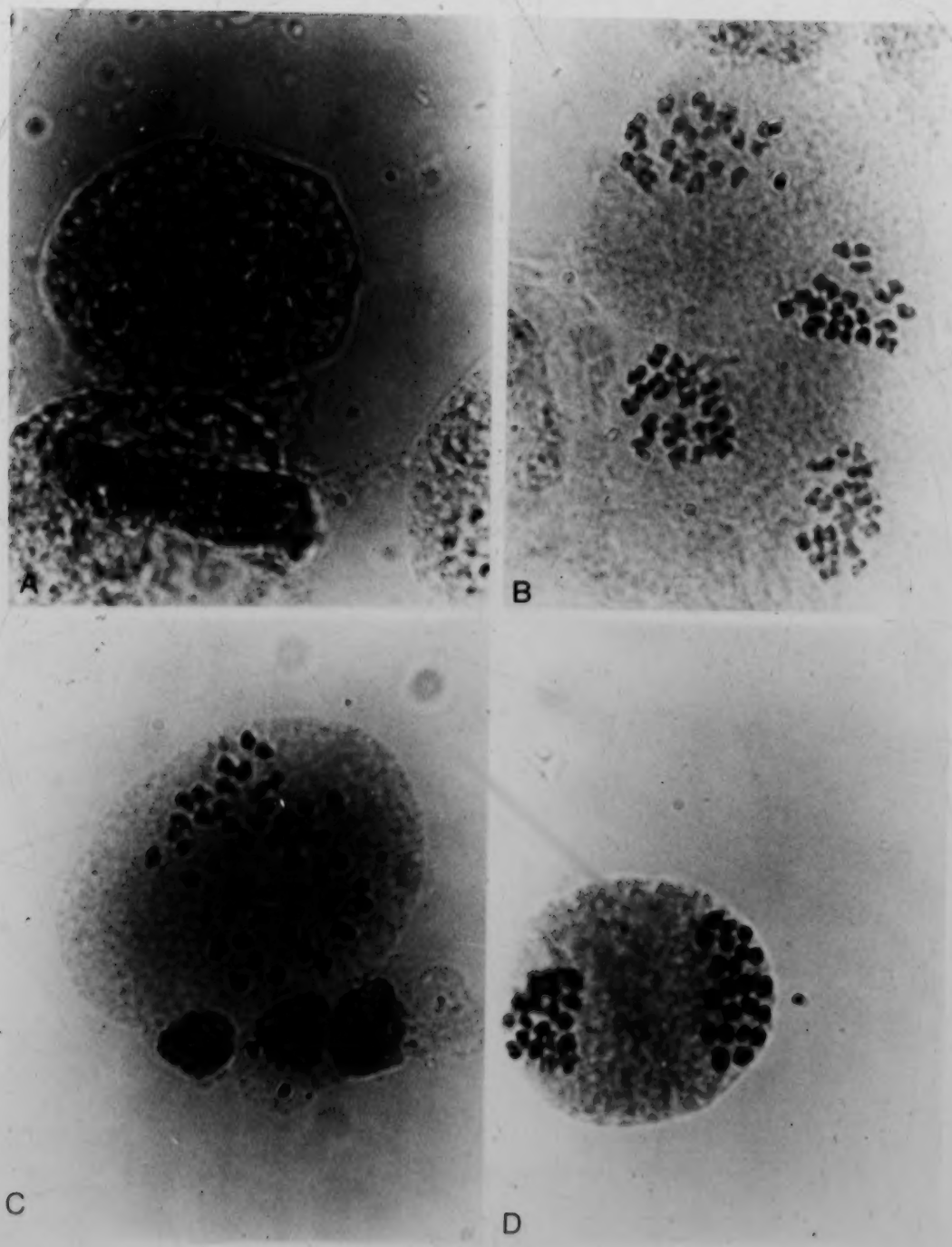
Figure 5 Meiotic chromosomes of aureoid *Senecio* species.

A. **n=23** *S. streptanthifolius* var. *borealis* (Bain 139)

B. **n=23** *S. streptanthifolius* var. *rubricaulis* (Bain 083)

C. **n=23** *S. tridenticulatus* Rydb. (Bain 098)

D. **n=23** *S. multilobatus* T. & G. (Bain 024)


A
B
C
D

present study show that tetraploid populations occur in two major regions. In one of the regions, an increase in ploidy level correlates well with previously recognized structural variation within the *S. streptanthifolius* complex. The synopsis of counts reported from the seven taxa of the *S. streptanthifolius* complex is followed by reports of counts from related species.

S. streptanthifolius var.*streptanthifolius*

Four counts of *S. streptanthifolius (s.s.)* are reported here. All are diploid. No apparent structural differences exist between the tetraploid collection (NA4869) cited by Morton (1981) and diploid populations from the same region.

S. streptanthifolius var. *borealis*

Ten counts of var. *borealis* are reported from populations throughout western Canada and the northwestern United States. With the exception of one possible hybrid population which is tetraploid, all others are diploid.

S. streptanthifolius var.*rubricaulis*

Eight counts were made from this variety. Four are diploid and four are tetraploid. Three of the tetraploid populations -- two from the Wasatch Mountains in Utah and one from the Wind River range in Wyoming -- are easily referrable to the *platylobus* segregate of the *rubricaulis* phase as interpreted by Barkley (1962). The fourth population (Bain 107) has deeply dentate but not lobate leaves. It was growing on a disturbed roadbank and showed pronounced vegetative reproduction from horizontal rootstocks.

Three of the four diploid populations were collected in Summit County, Utah while the fourth is from Teton County, Wyoming. The same pattern apparent in the tetraploids holds true in the diploids. The more southern populations have more lobate leaves while the leaves of the northern populations are sharply dentate.

S. oodes

Four counts were made from *S. oodes*, three from typical populations and one from a predominantly discoid population. They are all diploid.

S. laetiflorus

One count was made from *S. laetiflorus* in northern California. It is also diploid. In addition, after examining the voucher specimen (Ornduff 6269 UC), it was determined that one of the previously reported diploid counts from *S. streptanthifolius* in the literature (Ornduff *et. al.*, 1967) is actually from a population of *S. laetiflorus*

S. wallowensis

One count was made from a population of *S. wallowensis* collected from the Wallowa Mountains in Oregon. It is diploid. In addition, the guard cell sizes of three other populations were compared to values for diploid and tetraploid *Senecio* species. Two of the populations are apparently diploid while the third is apparently tetraploid. See Table 11.

S. kluanei

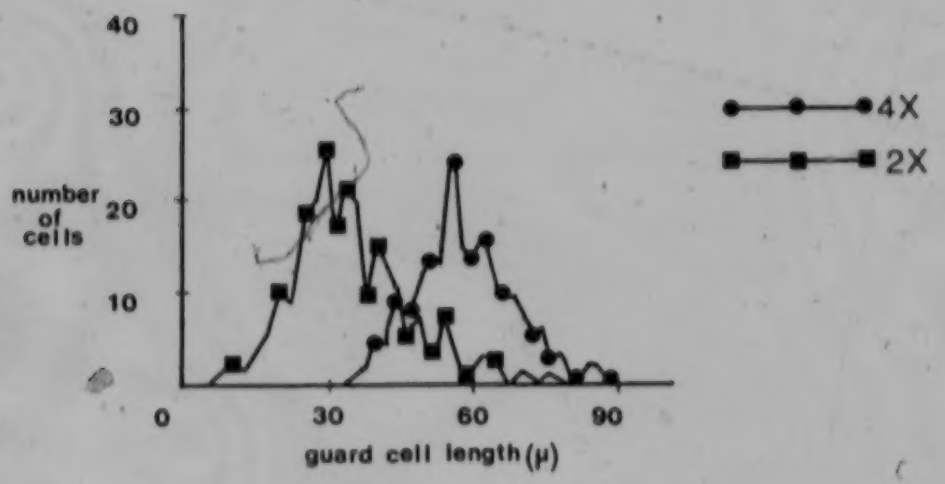
Counts were made from three populations of this species. All are tetraploid. The populations were all found growing on dry, open, disturbed roadsides. Field observations of one population (Bain 152) suggest that it had a high proportion of monocephalous plants.

S. neomexicanus

Previous chromosome reports have all been diploid (±2) for this complex. Nine new counts are presented including two from tetraploid populations. Barkley (1978, 1980) divided this polymorphic species into four varieties, all of which have some geographical integrity and all of which were previously described as species. *S. neomexicanus* var. *mutabilis*, [*S. mutabilis* according to Barkley (1968a)], introgresses with a number of other taxa including *S.*

Table 11. Guard cell measurements in the *S. streptanthifolius* complex

A. Differences in guard cell length between known diploid and tetraploid populations.



Collection	N	mean (μ)	t-value (vs. 2Xstd.)	significance	t-value (vs. 4Xstd.)	significance
Diploid(2X)std.	253	36.21			22.63	>.0005
Tetraploid(4X)std.	199	48.57	22.63	>.0005		

B. Guard cell lengths from populations of unknown chromosome number.

S. wallowensis

Collection	N	mean (μ)	t-value (vs. 2Xstd.)	significance	t-value (vs. 4Xstd.)	significance
Peck 17651	50	46.96	11.33	>.0005	1.91	0.1
Williams 78-248-7	52	37.48	1.41	0.2	14.20	>.0005

S. streptanthifolius var. *borealis*

Collection	N	mean (μ)	t-value (vs. 2Xstd.)	significance	t-value (vs. 4Xstd.)	significance
Hitchcock & Martin 7409	54	36.71	0.560	<.02	15.44	>.0005

streptanthifolius. Three chromosome counts from populations of var. *mutabilis* in southeastern Utah and southwestern Colorado, (Bain 022, 093, 094), indicate that it is diploid. Two counts from *S. neomexicanus* var. *metcalfei*, which structurally resembles *S. tridenticulatus*, both indicate that this taxon is tetraploid. The other two varieties, var. *neomexicanus* and var. *toumeyi*, are both apparently diploid.

The reported existence of aneuploidy in this species (Morton, 1981) is not corroborated by the present study.

S. pauperculus

Many diverse chromosome numbers have been reported for this species. (Table 3, Introduction). The general aureoid pattern of n=22 in the east and n=23 in the west is not as evident in the reports of this species. In the west alone, numbers ranging from n=20,22,23,44 and 46 have been reported. Of the eleven new counts reported here, seven are from tetraploid populations, (n=46), and three are from diploid populations, (n=23). With one exception, all of the Alberta populations as well as those from the Northwest Territories are tetraploid. Of the three diploids, two are from northern British Columbia in the Summit Lake area and one is from southern Idaho. One tetraploid population from Idaho may represent a hybrid between *S. pauperculus* and *S. streptanthifolius*.

S. canus

Like *S. pauperculus*, *S. canus* has a wide range of previously reported chromosome numbers reflecting three ploidy levels. Previous reports indicate that it is diploid in Oregon, Idaho, California, Montana and Wyoming; tetraploid in Oregon, California, Nevada and British Columbia and hexaploid in Alberta. Although *S. canus* exhibits a diversity of chromosome numbers and is geographically wide-ranging, it is an unusual aureoid species in that it is relatively uniform structurally. The ten counts presented here also span three ploidy levels. The three diploid counts are all from Oregon. Of the five tetraploid counts, two are from Oregon, two are from Alberta and one is from California. The

two hexaploid populations are from Alberta and British Columbia. The two tetraploid populations from Alberta represent a substantial range extension for the tetraploid race from its essentially west coast and southwestern distribution. The previous report of hybridization between *S. canus* and *S. streptanthifolius* (Ornduff, 1967) is not corroborated by this study. A collection was made from the vicinity reported for the hybrid (Longview, Alberta) and attempts were made to find plants which were structurally intermediate between *S. canus* and *S. streptanthifolius*. The resulting chromosome counts, however, were always n=*ca.*69 with no apparent univalents.

S. tridenticulatus

Only one count is presented from this study. It is from a diploid population in Colorado and as such it conforms with the three previously reported diploid counts for the species.

S. fendleri

All previous counts of *S. fendlerii* are diploid. The two new counts presented here are also diploid. One of the two populations counted was growing sympatrically with a population of *S. streptanthifolius*. Two plants grown in the greenhouse from seed of this *S. streptanthifolius* population exhibit structural characteristics intermediate between *streptanthifolius* and *fendleri*. As in both putative parents the chromosome number of the intermediate is 2n=46.

The present study points to a high degree of chromosomal stability within the complex. Although all of the large species complexes examined exhibit multiple ploidy levels, no evidence for aneuploidy, b-chromosomes, univalents or other similar chromosome anomalies was found.

C. Flavonoid Chemistry

Thirty-five flavonoid glycosides were isolated from the *S. streptanthifolius* complex and related species. Six of the compounds are flavone glycosides; the rest are flavonol glycosides. Chromatographic and spectral data for the 35 compounds are presented in Table 12. A composite two-dimensional chromatogram of all the compounds is presented in Figure 6.

Most of the differences between flavonoids present in the complex are found in the sugar fraction of the molecules. The five sugars most commonly associated with flavonoids: glucose, galactose, arabinose, xylose and rhamnose are all present in various combinations. In addition, sugars may vary with respect to their point of attachment on a flavonoid molecule. They are most commonly found either at the 3 position, the 7 position or at both. The flavonoids of this complex show all three attachment patterns.

The sugar molecules associated with a given flavonoid base molecule showed wide variation both inter- and intra-specifically. In order to express the variation in the most manageable fashion, the flavonoid characters were defined using only three criteria:

1) type of flavonoid base molecule, *e.g.* quercetin, kaempferol, luteolin, *etc.*
2) point(s) of sugar attachment, *e.g.* 3 or 7 position, or both
3) the number of sugars attached, *e.g.* one, two or more.

Where sugars are attached at both the 3 and the 7 position, no further subdivision of the class based on the number of sugars attached at each position was made. In this way the twelve classes presented in Table 13 were derived. A complete listing of flavonoids present in the complex may be found in Table 12. Some of the more prevalent compounds will be referred to by name in the text.

The most common flavonoids in the complex are the quercetin 3-O glycosides which is not surprising since they are common throughout the angiosperms. Quercetin 3-O mono- and di-glucoside as well as quercetin 3-O arabinoside are the three most common compounds.

Table 12. Chromatographic, spectral and Rf data for the flavonoid glycosides of *Senecio*

Compound [1]	λ max. nm [2] 100%MeOH				λ max. nm					colours[3] at 350 nm			Rfs[3] X 100			
					NaOMe	AlCl$_3$	AlCl$_3$–HCl	NaOAc	H$_3$BO$_3$	UV	UV/NH$_3$	UV/NA[4]	BAW	H$_2$O	15%HOAc	PhOH
	Band II		Band I		Band I	Band I	Band I	Band II	Band I							
Q 3-O arab	256	274s	354	298s	+64	+72	+42	+12	+18	P	Y	O	69	11	35	51
Q 3-O di-arab	256	268s	354	299s	+70	+70	+40	+12	+9	P	YG	O	41	18	50	56
Q 3-O sophoroside	258	275s	358	298s	+54	+54	+17	+12	+20	P	Y	O	41	33	62	53
Q 3-O arab,glu	255		350	296s	+75	+82	+48	+15	+22	P	Y	O	46	21	51	65
Q 3-O glu	258		362	302s	+64	+72	+58	+16	+20	P	Y	O	60	9	41	51
Q 3-O glu,xyl	258	269s	356	301s	+54	+82	+46	+14	+18	P	Y	O	69	12	45	72
Q 3-O arab,glu,xyl	260	270s	359	301s	+73	+75	+43	+14	+19	P	Y	O	61	9	38	56
Q 3-O rut	258	266s	358	302s	+40	+72	+52	+6	+16	P	Y	O	47	24	52	50
Q 3-O tri-arab	258	266s	362	298s	+64	+72	+40	+30	+18	P	Y	O	43	54	39	40
Q 3-O gentiobioside	258		352	268s	+44	+56	+20	+12	+20	P	Y	O	40	26	46	39
Q 3-O rut 7-O gal	266		360		+62	+82	+40	+3	+10	P	Y	O	—	—	—	—
Q 3-O glu,arab 7-O xyl	255	270s	345		+65	+77	+50	+10	+13	P	Y	O	37	30	54	23
Q 3-O glu 7-O xyl	256	268s	350		+64	+80	+46	+10	+44	P	Y	O	38	25	54	15
K 3-O glu	268		350		+50	+52	+48	+6	+6	P	G	G	74	14	47	58
K 3-O arab	266		344		+62	+55	+55	+6	+4	P	G	G	69	15	46	75
K 3-O glu,gal	255		346		+56	+52	+50	+17	+4	P	G	G	68	13	41	75
K 3-O glu,arab	268		350		+48	+50	+46	+7	+6	P	G	G	61	52	48	40
K 3-O glu 7-O rhm	266		348	315s	+50	+50	+50	0	+4	P	G	G	52	37	59	79
K 3-O rut 7-O gal,arab	267		348	310s	+37	+54	+52	0	+5	P	G	G	57	30	63	76
Iso 3-O arab,glu	256	268s	358		+50	+44	+44	+18	+4	P	Y	Y	60	9	39	26
Iso 3-O glu,gal	256		356		+50	+42	+40	+14	+6	P	Y	Y	52	14	42	37

Compound [1]	λ max, nm [2]			λ max, nm					colours [3] at 350 nm			Rfs [4] X 100			
	100%MeOH			NaOMe	$AlCl_3$	$AlCl_3$–HCl	NaOAc	H_3BO_3	UV	UV/NH,	UV/NA [5]	BAW	H_2O	15%HOAc	PhOH
	Band II		Band I	Band I	Band I	Band I	Band II	Band I							
Iso 3-O arab,glu,rhm	255	268s	349	+76	+63	+53	+19	+15	P	Y	Y	50	26	50	36
Iso 3/7 glu	258		350	+46	+42	+42	+4	+2	P	Y	Y	26	28	57	45
Iso 3/7 glu	254		356	+50	+39	+39	--	--	P	Y	Y	26	40	67	39
Iso 3/7 glu	258		354	+64	+48	+48	0	+2	P	Y	Y	38	30	66	40
Iso 3/7 glu	252	266s	356	+72	+38	+38	0	0	P	Y	Y	24	27	63	40
Iso 3/7 arab	258	269s	352	+58	+35	+34	-2	+11	P	Y	Y	35	16	48	35
Iso 3-O di-glu 7-O arab	254	265s	346	+56	+56	+56	+4	+6	P	Y	Y	23	67	63	32
Iso 3-O rut 7-O arab,glu	258	266s	348	+34	+12	+10	0	+4	P	Y	Y	53	21	52	35
L? 7-O arab	270		330	+70	+74	+20	0	-80	P	Y	O	73	14	43	35
L? 7-O arab,glu	276		338	+80	+66	+26	-4	+38	P	Y	O	40	50	43	45
L? 7-O di-glu	270		330	+96	+106	+28	+2	+44	P	Y	O	57	48	51	28
L? 7-O arab,glu,rhm	270		332	+90	+78	+68	+4	+28	P	Y	O	62	67	48	34
A 7-O glu	268		338	+74	+66	+66	+7	+20	P	YG	G	78	7	34	56
A 7-O xyl	266		332	+76	+30	+21	-4	+24	P	YG	G	65	9	39	42

[1]Compounds: A = Apigenin, K = Kaempferol, L = Luteolin, Q = Quercetin, Iso = Isorhamnetin, arab = arabinose, gal = galactose, glu = glucose, rhm = rhamnose, rut = rhamnosylglucoside, xyl = xylose

[2]s = shoulder.

[3]Colour key: P = purple, Y = yellow, G = green, O = orange.

[4]NA = Naturstoffreagens A in MeOH.

[5]See text for solvent composition.

Figure 6. Composite chromatograph of the flavonoid glycosides of the *Senecio streptanthifolius* complex.

1 Iso 3/7 glu_2

2 Iso 3/7 glu_4

3 Iso 3-O di-glu 7-O arab

4 Iso 3/7 glu_1

5 Iso 3/7 glu_3

6 Q 3-O sophoroside

7 Q 3-O glu 7-O xyl

8 Q 3-O glu,arab 7-O xyl

9 Iso 3/7 arab

10 Q 3-O di-arab

11 Q 3-O gentiobioside

12 L 7-O arab,glu

13 Q 3-O tri-arabinoside

14 Q 3-O rutinoside

15 Q 3-O arab,glu

16 K 3-O glu 7-O rhm

17 Iso 3-O rut 7-O arab,glu

18 Iso 3-O arab,glu,rhm

19 Iso 3-O glu,gal

20 K 3-O rut 7-O gal,arab

21 L 7-O di-glu

22 K 3-O glu,arab

23 L 7-O arab,glu,rhm

24 Q 3-O glu

25 Q 3-O arab,glu,xyl

26 Iso 3-O arab,glu

27 K 3-O arab

28 Q 3-O glu,xyl

29 K 3-O glu,gal

30 A 7-O xyl

31 Q 3-O arab

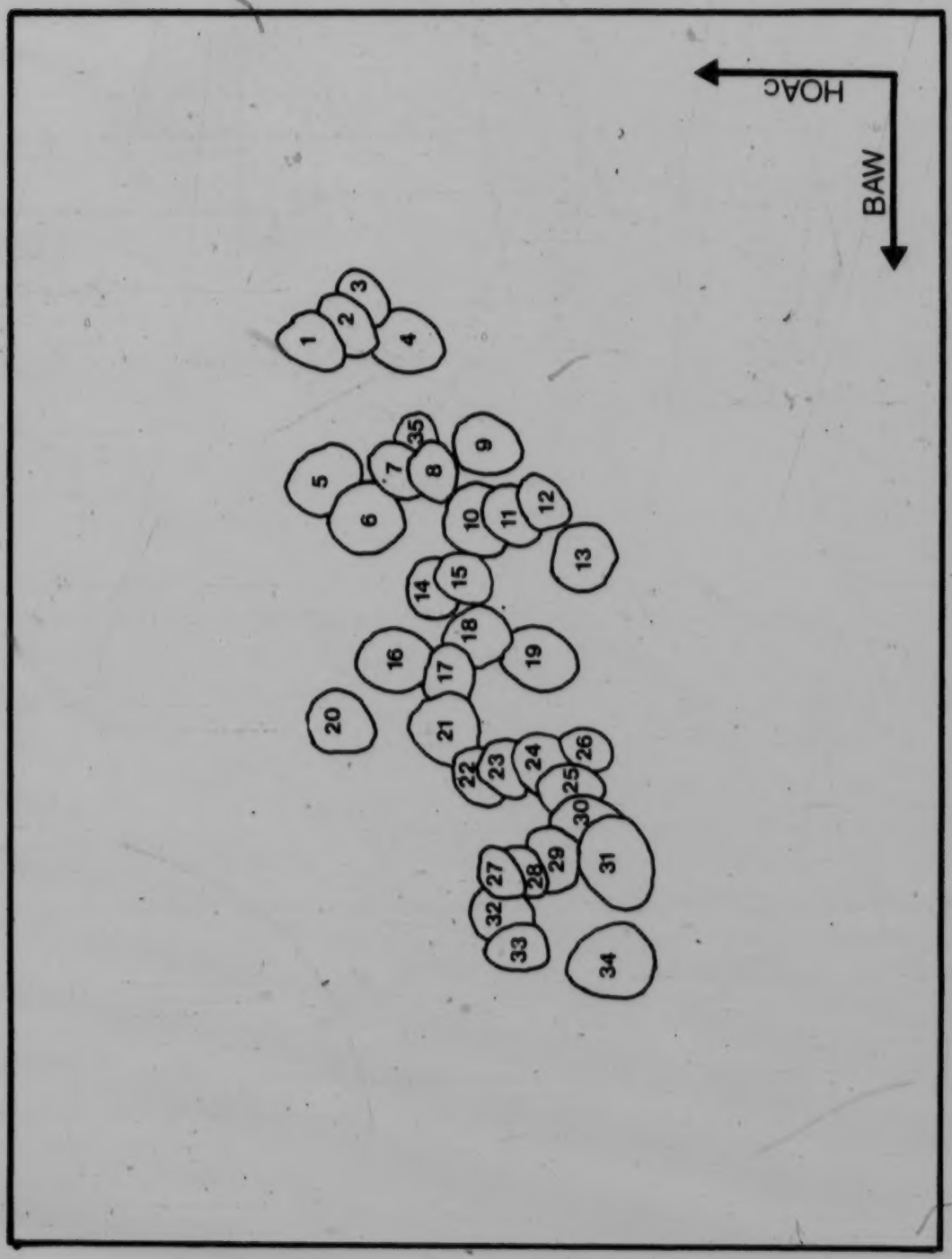
32 L 7-O arab

33 K 3-O glu

34 A 7-O glu

35 Q 3-O rut 7-O gal

Compounds: A = Apigenin, K = Kaempferol, L = Luteolin, Q = Quercetin, Iso = Isorhamnetin,
arab = arabinose, gal = galactose, glu = glucose,
rhm = rhamnose, rut = rhamnosylglucoside, xyl = xylose


HOAc
BAW
1
2
3
4
5
6
7
8
9
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35

Table 13. Distribution of flavonoid characters in the *S. streptanthifolius* complex and related species[2]

	S. strep. – varieties						other species					
	strep.	*boreal.*	*rubric.*	*laet.*	*oodes*	*kluanei*	*wall.*	*paup.*	*multi.*	*canus*	*neomex.*	*triden.*
Total populations surveyed	7	14	8	5	4	3	4	17	4	8	6	2
[1]Q-3-O mono-gly	7	13	3	–	3	2	–	–	2	5	6	–
Q 3-O di-gly	7	14	8	5	4	3	4	12	4	–	6	2
K 3-O mono-gly	5	–	7	–	4	3	–	–	2	–	–	–
K 3-O di-gly	–	–	5	–	–	3	–	–	–	–	–	–
Iso 3-O gly	–	–	–	5	–	–	4	–	–	–	–	–
L 7-O mono-gly	4	11	–	5	–	–	–	–	–	–	–	–
L 7-O di-gly	–	–	–	5	–	–	4	–	–	–	–	–
Q 3/7 gly	–	–	–	–	–	3	–	15	–	–	–	–
Iso 3/7 mono-gly	2	7	8	–	3	2	–	–	2	3	2	2
Iso 3/7 di-gly	–	11	–	–	3	–	–	–	–	5	–	2
K 3/7 gly	–	–	–	–	–	–	–	17	–	–	–	–
A 7-O gly	–	–	–	5	–	–	–	17	–	–	–	–
Total flavonoid characters/taxon	5	5	5	5	4	6	3	4	4	3	3	3

[1]Compounds: A = Apigenin, K = Kaempferol, L = Luteolin, Q = Quercetin, Iso = Isorhamnetin, gly = glycosides
[2]Taxa: *strep* = *streptanthifolius*, *boreal.* = *borealis*, *rubric.* = *rubricaulis*, *laet.* = *laetiflorus*, *wall.* = *wallowensis*, *paup.* = *pauperculus*, *multi.* = *multilobatus*, *neomex.* = *neomexicanus*, *triden.* = *tridenticulatus*,

When outlining trends in the flavonoid chemistry of the Compositae, Harborne (1977) describes three common patterns for leaf flavonoid constituents. They are:

1) the presence of common flavonol glycosides, *i.e.* quercetin and kaempferol,
2) the presence of common flavone glycosides, *i.e.* apigenin and luteolin,
3) the presence of C-glycosylflavones based on the two previously mentioned common flavones.

He further adds that the absence of C-glycosylflavones usually means that either pattern 1 or pattern 2 is adhered to with no overlap. This, however, was not always found to be the case in this study. Apigenin and luteolin derivatives were never found in great abundance but their presence was never without a complement of flavonols. Harborne goes on to describe four groups of rarer flavonoids which occur in the Compositae. The first group he refers to is the simple methyl ethers. The isorhamnetin (quercetin 3'-methyl ether) derivatives present in the complex fall into this category. The second group Harborne mentions contains the 6-hydroxylated compounds which, as their name suggests, possess a hydroxyl group rather than the more usual hydrogen at the 6 position. No compounds from this group were detected in this study. The final two groups, the highly methylated compounds and the highly glycosylated compounds respectively, are viewed by Harborne as mutually exclusive (with regard to their presence in any given plant). That is, the leaf flavonoids of a plant may either be bound in a lipid soluble form through a high degree of methylation or, they are present in the cell vacuole as water soluble glycosides; never both. This latter pattern has been the rule throughout the *S. streptanthifolius* complex. No highly methylated compounds were found; instead a wide array of sugars and glycosylation patterns were identified. With these general trends established what follows is a synopsis of the flavonoid patterns within each taxon. Discussion of the implications of these results will be withheld until a later section. It should be noted that the compounds identified as luteolin derivatives (L? in Table 12) are done so tentatively. Although the spectral data indicates that the compounds are

luteolin, the chromatographic data do not match very closely the few reports in the literature.

S. streptanthifolius

Seven flavonoids were identified from seven populations of var. *streptanthifolius*. As in var. *borealis*, there is a comparatively large number of simple quercetin 3-O glycosides. Both taxa also produce luteolin glycosides, as do *S. wallowensis* and *S. laetiflorus*. The primary chemical difference that exists between var. *streptanthifolius* and var. *borealis* is that var. *streptanthifolius* possesses one kaempferol glycoside, (kaempferol 3-O arabinoside), while kaempferol derivatives are completely absent from var. *borealis*. Kaempferol 3-O glycosides are found in the var. *rubricaulis* complex as well as in *S. kluanei*.

S. streptanthifolius var. *borealis*

Eight flavonoid glycosides, (seven flavonol, one flavone), were isolated from fifteen populations of this taxon sampled from the whole of the geographic range. Four quercetin 3-O glycosides, two isorhamnetin 3/7 glycosides, one quercetin 3/7 glycoside and one luteolin 7-O glycoside make up the full complement of the profile. Although quercetin 3-O arabinoside is the only compound that is ubiquitous, all of the others are widespread except quercetin 3/7 glycoside which is found in only three of the populations sampled. All three of these populations are from the northern British Columbia - Yukon area. This same compound is found in the tetraploid race from the southern Yukon but is absent from northern populations of var. *borealis* in the Northwest Territories. The implications of the distribution of this compound will be discussed in a later section. This was the only instance where the distribution of a compound was found to have any implications.

S. streptanthifolius var. *rubricaulis*

Seven flavonol glycosides were isolated from five populations of var. *rubricaulis*. Of the four ubiquitous compounds, two are kaempferol 3-O glycosides while one is a quercetin 3-O glycoside and one an isorhamnetin 3/7 glycoside. The three remaining compounds each appear only once in the survey and are not considered further. The difficulty associated with separating var. *rubricaulis* from var. *streptanthifolius* and *S. multilobatus* using morphology is also found when using flavonoid characters. All three groups have quercetin, kaempferol and isorhamnetin glycosides. Only var. *streptanthifolius* also has luteolin derivatives. The lack of difference between the profiles of the diploid and tetraploid *rubricaulis* races indicates that what has been called *S. platylobus* in the past may be a polyploid derivative of var. *rubricaulis*.

S. kluanei

Ten flavonoid glycosides were isolated from three populations of this geographically restricted taxon. This flavonoid profile is the most complex of all the taxa studied. Five quercetin 3-O glycosides, two kaempferol 3-O glycosides, two quercetin 3/7 glycosides and one isorhamnetin 3/7 glycoside were identified. Although morphology reveals a close relationship between this taxon and the diploid var. *borealis*, distinct chemical differences such as the presence of kaempferol 3-O glycosides and the complete absence of luteolin derivatives exist. These same two characters ally the northern tetraploid with more southern taxa such as var. *rubricaulis*.

S. wallowensis

Five flavonoid glycosides, (four flavonol, one flavone), were identified from five populations of this, another taxon with a restricted distribution. Four of the populations are from the Wallowa Mountains in Oregon and one is from Washoe County in Nevada, the only two areas where this species has been frequently collected. The species contains two quercetin 3-O glycosides, one luteolin glycoside and two isorhamnetin 3-O glycosides. These isorhamnetin glycosides are found in only one other taxon, *S. laetiflorus*, which, although it is usually

very ecologically distinct from *S. wallowensis*, is found in the same general geographic area, (Oregon and northern California). The absence of any isorhamnetin 3/7 derivatives is unusual in this complex; the only other taxon lacking them being *S. pauperculus*.

S. laetiflorus

Six flavonoid glycosides, (three flavonol, three flavone), were isolated from this taxon. The presence of three flavone glycosides, (two luteolin and one apigenin), very clearly distinguishes this species from any other in the complex, the most any other species has being one. Of further note is the already mentioned presence of isorhamnetin 3-O glycosides, a trait shared with *S. wallowensis*. Two quercetin 3-O glycosides round out the profile. *S. laetiflorus* contains an unusually large number of triglycosides (three different sugar molecules attached at one position). Three out of the four triglycosides isolated in the complex are found in *S. laetiflorus*, the fourth being found in *S. kluanei*. The possession of an apigenin derivative, apigenin 7-O xyloside, indicates a possible relationship with *S. pauperculus*, the only other taxon containing a similar compound.

S. oodes

Ten flavonol glycosides were isolated from four populations of *S. oodes*. Five of the compounds are isorhamnetin 3/7 glycosides, two are kaempferol 3-O glycosides and three are quercetin 3-O glycosides. The possession of a large number of isorhamnetin derivatives is shared by *S. canus* which has four. In addition to this, both taxa possess a characteristic phenolic acid which has a distinct colour and position in the two-dimensional chromatograms. The possession of kaempferol glycosides is characteristic of *S. kluanei*, *S. streptanthifolius* var. *rubricaulis* and one variety of *S. neomexicanus* (var. *metcalfei*). The large number and variety of flavonoid types present in *S. oodes* suggests that it may be a combination of diverse genotypes.

S. canus

Five flavonol glycosides were isolated from nine populations of *S. canus*, four of which are isorhamnetin 3/7 glucosides. These four compounds are separable primarily by their different Rf values. The differences in Rf values may result from different numbers of glucose molecules at each position and/or different linkages between the sugar molecules. The fifth flavonoid glycoside isolated, quercetin 3-O glucoside, is common throughout the complex. The sampled populations showed great variability based on their flavonoid profiles, with three populations from Oregon showing a complete absence of isorhamnetin glycosides. The only discernable trend is that populations from further north, (*i.e.* Alberta and British Columbia) had fewer glycosides.

S. neomexicanus

Senecio neomexicanus contains a total of eight flavonol glycosides. *S. neomexicanus* is a diverse assemblage most recently divided into four varieties. Variety *mutabilis*, which has been closely associated with *S. streptanthifolius*, contains three quercetin 3-O glycosides, none of which are unique to the taxon. Of the other three varieties only var. *metcalfei* varies appreciably from this pattern in that it also has two isorhamnetin glycosides and one kaempferol 3-O glycoside.

S. multilobatus

Five flavonoids were isolated from four populations of *S.multilobatus*, three quercetin 3-O glycosides, one kaempferol 3-O glycoside and one isorhamnetin 3/7 glycoside. *S. multilobatus* possesses one more quercetin 3-O glycoside, (quercetin 3-O glucoside), and one less kaempferol 3-O glycoside than does *S. streptanthifolius* var. *rubricaulis*.

S. tridenticulatis

Four flavonoids were isolated from two populations of *S. tridenticulatis*, three isorhamnetin 3/7 glycosides and one quercetin 3-O glycoside.

S. pauperculus

Six flavonoid glycosides, (five flavonol, one flavone), were isolated from seventeen populations of *S. pauperculus*. The flavonoid profile is easily differentiable from those of other taxa because it is the only one which contains any kaempferol 3/7 glycosides of which it has two. A further distinguishing feature of *S. pauperculus* is its possession of one apigenin glycoside. Apigenin is found in only one other taxon, *S. laetiflorus*, where it occurs as a different glycoside. *S. pauperculus*, like *S. canus*, contains only one quercetin 3-O glycoside. Unlike *S. canus*, it has no isorhamnetin derivatives, but instead has quercetin 3/7 derivatives. This latter trait is shared by *S. streptanthifolius* var. *borealis*.

The study indicates that while there is some degree of variation between populations, flavonoids are very useful in delimiting taxa in the *S. streptanthifolius* complex. The differences between taxa are not always definitive but when the complex is examined as a whole, the flavonoid patterns clearly fall into categories that are supported by morphology.

One of the initial reasons for studying the flavonoid constituents in the complex was to gain a better insight into the degree of hybridization taking place. The results presented here do not provide the clear insight sought. Although there was no clear case of an intermediate taxon having a flavonoid profile which combined the characters of two distinct parents, in many cases taxa shared traits of one or more related taxa. The sharing of apigenin derivatives between *S. laetiflorus* and *S. pauperculus* and the sharing of numerous isorhamnetin 3/7 compounds between *S. oodes* and *S. canus* are two good examples. These shared traits may indicate that the two taxa have a common lineage but they cannot be taken as proof of a hybrid origin.

In some instances the flavonoids may show phytogeographic relationships. The sharing of isorhamnetin 3-O glycosides by *S. laetiflorus* and *S. wallowensis* ties in closely with their geographical proximity. *S. kluanei* shares flavonoid

characters with more southern taxa suggesting that it may represent a disjunct population of some previous wider-ranging senecio. Further exploration of these ideas will follow in discussions of phylogeny and phytogeography.

D. Field and Greenhouse Observations

The following observations of a non-quantitative nature were made during field and greenhouse studies conducted.

Numerous populations of aureoid senecio species were grown in the greenhouse from achenes collected during the previous field season. The achenes always exhibited a high rate of germination after a short cold treatment (4 days at -5° C). Since the treatment was carried out routinely after an initial trial, no data were gathered concerning which species, if any, did not require a cold treatment

In no case did a plant undergo a change in structure which was evident when compared to field collections of the same population. The studies did show very clearly that populations of *S. pauperculus* (Bain 068,069,081) were capable of reproducing asexually very successfully via rhizomes. The one population of *S. dimorphophyllous* grown (Bain 104) was also similarly successful. With few exceptions, all populations flowered on numerous occasions with no interim cold treatment or changes in photoperiod. *S. pseudaureus* var. *pseudaureus* (Bain 073) never flowered despite numerous cold treatments and *S.pseudaureus* var. *flavulus* (Bain 099) flowered once in three years. *S. moresbiensis* (Bain 112) and *S. ogotorukensis* (Bain 143) were both transplanted from the field; neither flowered. All populations exhibited limited or no fertility when grown under greenhouse conditions even when crosses were made between plants of the same population. One artificial cross between *S. oodes* (Bain 105) and *S. multilobatus* (Bain 087) produced four apparently viable achenes. Of these, two germinated and the resulting plants were grown to flowering stage. Both plants possess completely viable pollen as determined by staining tests. Further crossing experiments were abandoned because fertility was so uniformly

low, apparently for other than genetic reasons.

Numerous insect pollinators were observed visiting *Senecio* flowers in the field. They included bees, butterflies, and flies. The same insects were observed to visit the flowers of other plant species both before and after visits to *Senecio* flowers. In short, *Senecio* pollination showed no apparent insect specificity.

The achenes of *Senecio*, like those of most other Composite genera, were observed to be easily dispersed by the wind. Their small size and pappus of copious bristles greatly enhances their dispersability.

IV. Phylogeny

It is with some trepidation that I embark upon a discussion of the phylogeny of the *S. streptanthifolius* complex. Phylogenetic inferences are in my opinion more easily derived when taxa can be clearly and unambiguously defined. If that condition were even close to true for the *S. streptanthifolius* complex then this study would never have been undertaken. Wagner (1980) emphasized the point that "correct phenetic classification underlies any phylogenetic analysis". He went on to point out specific, serious problems one may encounter when constructing a cladogram and states that "in actively evolving groups, the evolutionary processes may be so randomized and unpatterned that they resist analysis". It is important to note that he chose *Senecio* as his example of just such a group, stating "*Senecio* possesses a bewildering array of repetitive forms (and) has been estimated to contain as many as two or three thousand species". He concluded by saying that cladograms in such groups may be less reliable than in those groups that appear to have discrete lines of evolution, *i.e.*, the Magnoliaceae. Wagner's words of warning are not to be taken lightly. The problems that exist include the reliable determination of apomorphies and, perhaps more fundamentally, the assurance of monophyly. Establishment of the latter criterion certainly makes solving the former problem easier; therefore monophyly, as it pertains to the *S. streptanthifolius* complex, will be discussed first.

A **monophyletic group** as defined by Wiley (1980) is composed of an ancestral species, hypothetical or real, and all descendants of that species. Another term for a monophyletic group is a **clade**. Based upon chromosome number and other structural characters the aureoid senecios as a whole can reasonably be considered a monophyletic group. Beyond this however, notions of monophyly within the group are difficult to support. The traditional separation of the aureoid group into *Aurei*, *Tomentosi*, and *Lobati* is compromised by the presence of anomalous taxa in all groups as well as hybridization between the three groups. Taxa within the three groups are sufficiently similar that Barkley (1978) was able to name two species (*S. pauperculus* and *S. streptanthifolius*) as the focal points for variation within the whole complex. Clearly, in order to

attempt to construct a phylogeny of the *S. streptanthifolius* complex, some bold assumptions must be made at the outset. The first of these is that the *S. streptanthifolius* complex represents a monophyletic group. Support for this assumption comes indirectly from Barkley (1978), who described the complex as a single species, and from the present study where the numerical analysis on only two occasions (out of eighty-five) clustered OTUs from outside the complex in the same cluster as those from within. The suite of synapomorphies describing the presumed monophyletic *S. streptanthifolius* complex is:

i. leathery, turgid, oblanceolate to ovate, sub-entire leaves

ii. glabrous achenes

iii. fibrous root stock

Although these characters give a good approximation of the complex, it should be noted that the definition of more precise synapomorphies depends upon sister group comparisons derived from a cladistic analysis of the whole aureoid complex.

The next step after determining monophyly for a group is to designate the apotypic or derived states in the various character transformation series present.

It is not unreasonable to assume, in the phylogenetic analysis of a complex which can arguably be treated as one species, that distinguishing characters, not to mention derived characters (or apomorphies), may be difficult to find. The present study has alleviated that problem to some degree by providing a set of previously undetermined flavonoid characters. These flavonoid characters were used to construct a cladogram separate from one constructed using structural characters. Flavonoid characters were analyzed separately because it was felt that outgroup comparison was more easily and reliably done for the flavonoid compounds. The summaries of Robins (1977) for the tribe Senecioneae and Harborne (1977) for the Compositae were used as sources for character comparison in the flavonoid analysis. Thus the rest of the Senecioneae and the Compositae became the respective outgroups consulted. Through this method the structural cladogram could be compared with the flavonoid cladogram and

apparent contradictions re-examined.

Within the tribe, the apigenin and luteolin derivatives isolated have so far all been monoglycosides. Therefore flavone di- and triglycosides are considered to be derived. For the same reason, di- and triglycosides of the three flavonol types, quercetin, kaempferol and isorhamnetin, are all considered derived. Flavonol 3/7 glycosides have not been reported from the Senecioneae (Robins, 1977). Their occurrence here, therefore, is also considered to be a derived character. Additionally, by applying a previous argument, we can presume that flavonol 3/7 di= and triglycosides are derived when compared to flavonol 3/7 monoglycosides.

In some cases character trends are not evident from review papers where lists of compounds isolated are given. Such a case is the trend toward increasing numbers of flavone molecules in a species profile. The appearance of flavones has previously been correlated with a loss of woodiness (Bate-Smith, 1962; Harborne, 1972). This has led to the inference that the replacement of flavonols by flavones is an advanced trait. Just what advantage a flavone glycoside confers on an organism that a flavonol glycoside does not is a question raised by Swain (1977) and to which there still apparently is no answer. Furthermore, an association with woodiness may be of no importance when evaluating the character within the context of this study since woodiness is a trait not even remotely associated with this group. On the other hand, if we employ the same method of correlating the character transformation with one of known direction, this time within the *S. streptanthifolius* complex, we may gain more insight. In this case the transformation series of known direction is that from diploidy to polyploidy, polyploidy being the known apotypic state. Since polyploidy and flavone loss are directly correlated in the *S. streptanthifolius* complex, they are both considered to be apotypic.

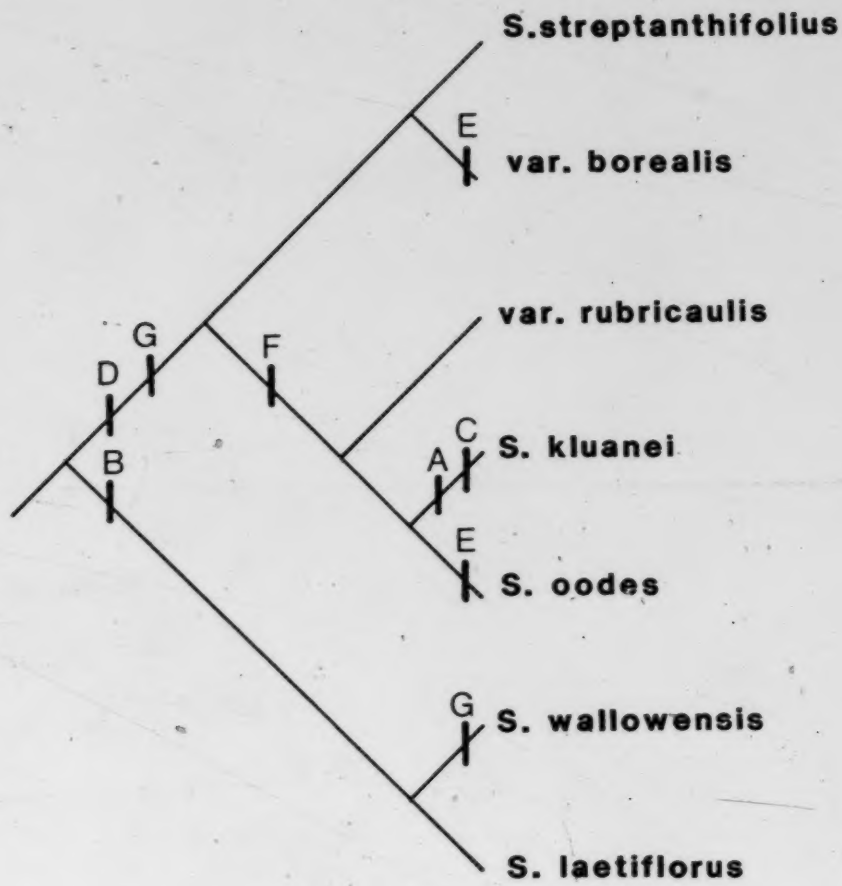
Using these guidelines, apotypic flavonoid characters were chosen and a cladogram constructed (see Figure 7 for characters and cladogram).

Figure 7. A hypothesis of the relationships within the *S. streptanthifolius* complex as shown by flavonoid apomorphies

	A	B	C	D	E	F	G
S. streptanthifolius	–	–	–	+	–	–	+
var. *borealis*	–	–	–	+	+	–	+
var. *rubricaulis*	–	–	–	+	–	+	+
S. oodes	–	–	–	+	+	+	+
S. kluanei	+	–	+	+	–	+	+
S. wallowensis	–	+	–	–	–	–	+
S. laetiflorus	–	+	–	–	–	–	–

Apomorphies

A K 3–O diglycosides
B L 7–O diglycosides
C Q 3/7 glycosides
D Iso 3/7 glycosides
E Iso 3/7 diglycosides
F Luteolin loss
G Apigenin loss



Structural Cladogram

A list of the apotypic structural characters used and the rationale employed in designating them as such follows.

By correlating the occurrence of weediness with the apotypic character annual life-form, we may conclude that weediness in North American senecios is also apotypic. Those species documented as occupying open disturbed habitats are defined as 'weedy' in this study.

Leaf dissection and leaf pubescence are both characters common in, and to some degree definitive of, other aureoid species complexes, (*e.g., Lobati* and *Tomentosi*). They are uncommon, and therefore considered derived, within the *S. streptanthifolius* complex. A further point of evidence for considering these characters apotypic is that a seedling's leaves resemble those of mature *S. streptanthifolius* irrespective of whether the seedling will mature into a pubescent or dissected-leaved plant. Support for this view comes from the application of Haeckel's Biogenetic Law as restated by Nelson and Platnick (1981).

> "Given an ontogenetic character transformation from a character observed to be more general to a character observed to be less general, the more general character is primitive and the less general advanced."

Increased head number has been cited by Cronquist (1955) as a general apotypic trend within the Compositae. Wolf (1981) concurs with this view with reference to *Arnica* subg. *Austromontana*. The same view is adopted for this study. Polyploidy is also considered apotypic however separate polyploidization events are treated as separate apomorphies and not parallelisms. A table of character values and the resulting cladogram appears in Figure 8.

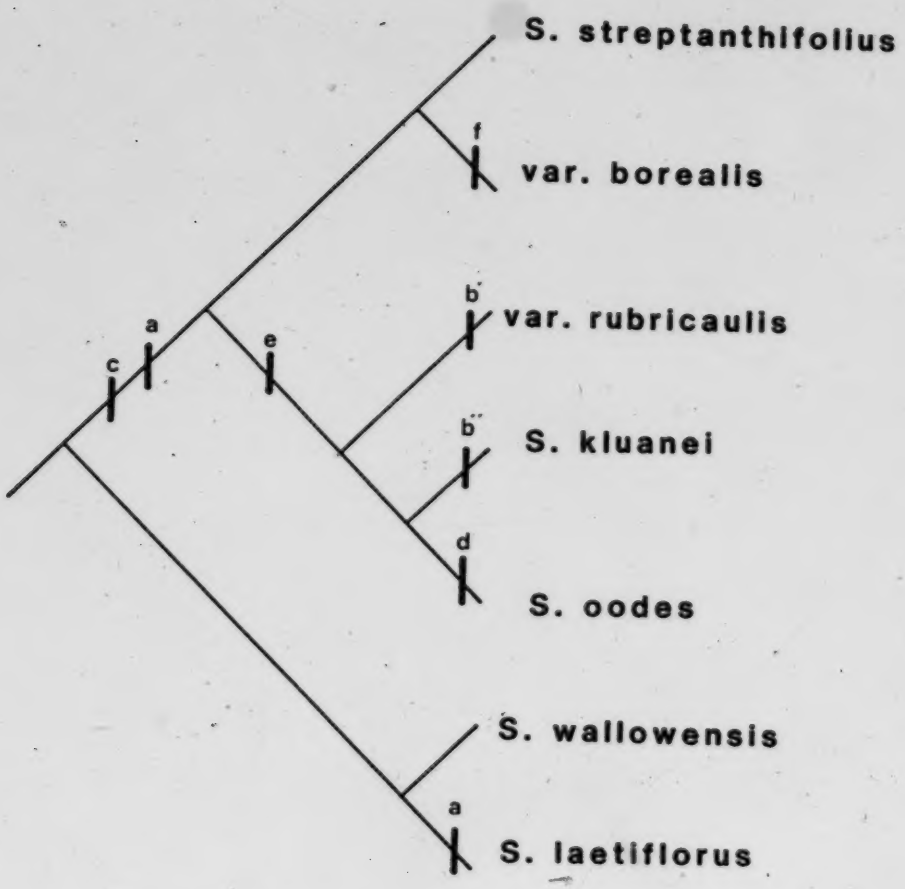
When comparing the structural and the chemical cladograms, it is immediately apparent that the two are very similar. In each case *S. wallowensis* and *S. laetiflorus* are separated together on one 'clade' and in each case the

Figure 8. A hypothesis of the relationships within the *S. streptanthifolius* complex as shown by structural apomorphies

	A	B	C	D	E	F
S. streptanthifolius	+	−	+	−	−	−
var. *borealis*	+	−	+	−	−	+
var. *rubricaulis*	+	+	+	−	+	−
S. oodes	+	−	+	+	+	−
S. kluanei	+	+	+	−	+	−
S. wallowensis	−	−	−	−	−	−
S. laetiflorus	+	−	−	−	−	−

Apomorphies

A head number
B established polyploidy
C weedy habit
D leaf pubescence
E leaf dissection
F sub-spatulate leaves



latter two taxa have the fewest apotypic characters. Another similarity between the two is the joining of *S. streptanthifolius* var. *streptanthifolius* and var. *borealis* on the same clade. Finally, in each cladogram, the sister group of the var. *streptanthifolius* - var. *borealis* clade contains the other three taxa. In fact, the only real difference between the two cladograms is the reversal of positions for *S. oodes* and *S. kluanei* in relation to var. *rubricaulis*.

Given that the two cladograms are so similar, what is the implication? Platnick and Nelson (1981) provide a stimulating discussion of this question and end up by concluding that when there is some "replication or combinability between two independently derived cladograms, it represents an estimate of the one cladistic parameter which applies to the group in question." That being the case, the removal of var. *rubricaulis* would result in the remainder of the cladogram being a good estimate of the cladistic parameter applicable to the six remaining taxa; that is, providing the assumptions regarding monophyly and apomorphy which were made at the outset are correct. Removal of var. *rubricaulis* should have been done at the outset according to Wagner (1980) based on the premise that it is a hybrid taxon. According to Wagner, because hybrids have more than one phylogenetic parent they cannot be plotted in the same manner as species. The hybrid nature of var. *rubricaulis* has been postulated in the past (Barkley, 1962) based on structure and distribution. Nothing in the current study, including flavonoid profiles, refutes this notion and perhaps the reporting of tetraploids within the group may be considered as supporting it. A hybrid origin may also be considered for *S. oodes* and *S. kluanei* although the putative parents in each case (*S. canus* and *S. pauperculus*, respectively) are somewhat more obscure. In all three cases the other putative parent (besides *S. streptanthifolius*) is outside the *S. streptanthifolius* complex and therefore not represented in the cladogram. Therefore, considering the potential hybrid nature of all three taxa, some alterations in the cladogram may be appropriate. As it stands now the cladogram indicates that after the initial speciation event which separated the *S. laetiflorus* - *S. wallowensis* line, a second split occurred with *S. streptanthifolius* and var. *borealis* separating on

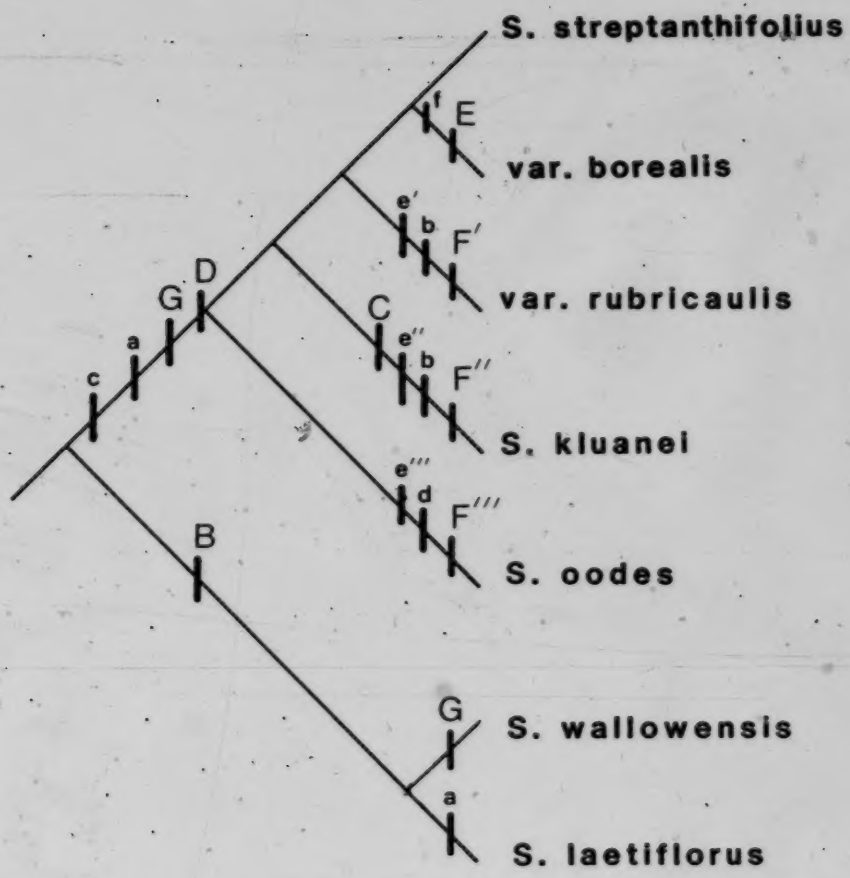
one branch or clade, *S. kluanei*, *S. oodes* and *S. streptanthifolius* var. *rubricaulis*, on the other. This latter clade (including the common ancestor of the three taxa) must have had an extensive north-south distribution at one time in order to have given rise to three such geographically diverse taxa. This would also mean that *S. streptanthifolius*, which has in the past been thought to be the general, wide-ranging species encompassing the other taxa as local variants, is itself a relatively restricted taxon. Acceptance of this scenario would necessitate the elevation of var. *rubricaulis* to species rank on a purely phylogenetic basis since its maintenance as a variety would render *S. streptanthifolius* paraphyletic.

On the other hand, a re-evaluation of the apotypic characters defining this third clade may be necessary in light of possible separate hybrid origins of the three taxa. The synapomorphy leaf dissection shared by these taxa may not be the result of a single speciation event but rather the three different patterns of leaf dissection may have arisen three different times. The character, as it is outlined now, makes no reference to dissection pattern and as such, is quite broadly defined. It is not unreasonable to assume that the even dentation of the *S. oodes* leaf margin may have a totally different origin from either the deep, irregular dentation and lobing of the var. *rubricaulis* leaf, or the serrate-dentate margins of the *S. kluanei* leaf. Similarly, it may be incorrect to consider the pubescence of leaf and involucre head present in *S. oodes* as comparable to the sparse pubescence present at the base of the involucre of *S. kluanei*. The changes in the cladogram brought about by considering leaf dissection a separate apotypic character in each taxon would result in the cladogram presented in Figure 9 which combines both flavonoid and structural characters.

This cladogram represents an improvement since it maintains *S. streptanthifolius* as a monophyletic group. Although *S. kluanei* and *S. oodes* are placed in a given sequence on the cladogram, no clear inference can be made with respect to their relative ages. Thus, based on the evidence presented, the order could have as easily been switched.

Figure 9. A re-evaluation of the relationships within the *S. streptanthifolius* complex using both structural and flavonoid characters

the characters are the same as those in Figures 7 and 8 with two exceptions:
1. leaf dissection has been separated into three distinct apomorphies (e', e'', e'''),
2. luteolin loss has similarly been separated into three apomorphies (F', F'', F''').



Re-examination of the chemical cladogram is also necessary and again the variability within each of the categories defined as characters provides information resulting in an alternative viewpoint.

The synapomorphy, **luteolin loss**, which groups *S. oodes*, *S. kluanei* and var. *rubricaulis* may have been derived on separate occasions through hybridization, in exactly the same fashion that leaf dissection is considered to have had multiple origins. Of the three putative parents (other than *S. streptanthifolius*) involved in these hybridization events, none contain luteolin derivatives. Thus hybridization may have easily resulted in three separate eliminations of luteolin from the resulting hybrid taxon. Furthermore *S. oodes* and *S. kluanei* each show positive correlations with their putative parent species based on additional flavonoid characters. *Senecio oodes* and *S. canus* each have a large number of isorhamnetin 3/7 glycosides ($\geq$4) whereas all other taxa surveyed have no more than two. *Senecio kluanei* and *S. pauperculus* are the only two taxa surveyed that have quercetin 3/7 glycosides.

It is clear from the evidence presented that an alternative explanation to the original cladogram is possible. This alternative explanation is favoured over the initial one whereby an ancestral species different from *S. streptanthifolius* was wide-ranging and gave rise to *S. oodes*, *S. kluanei* and var. *rubricaulis* mainly because there is no evidence for this ancestral species ever existing in the range to which it is ascribed. The ancestral species would either have to have resembled one of the three derived species (and since no taxon that resembles any of the derived species comes close to occupying the combined range of the three this seems unlikely), or it would have to have resembled extant *S. streptanthifolius*, the species which embodies most of the common characters. It would not be parsimonious to postulate a *S. streptanthifolius*-like ancestor which then gave rise to three separate taxa (for a total of four speciation events) when apparently *S. streptanthifolius* itself through hybridization (not an uncommon phenomenon in the aureoid complex according to Barkley, 1978) can explain the events as well in only three steps.

It still remains contradictory to postulate three more or less similar hybridization events and yet treat two of the resulting taxa as species while calling the third a variety. Such a contradiction can only be resolved by returning to the phenetic results and examining them.

It has already been stated that both structural and distributional data support the idea that var. *rubricaulis* is of hybrid origin, arising from *S. streptanthifolius* and *S. multilobatus*. Additionally, var. *rubricaulis* exhibits some localized variation. Populations in Idaho and Wyoming tend to have leaves that are deeply dentate rather than lobate. Populations in the Wasatch Mountains of Utah vary greatly in size depending upon location. The existence of both diploid and tetraploid populations further complicates the picture. Furthermore the ploidy differences cannot always be reliably correlated with structural features. This complicated variation pattern supports the suggestion of Barkley (1962) that var. *rubricaulis* "represents a series of persistent introgressants (between *S. streptanthifolius* and *S. multilobatus*)". Furthermore, the more entire-leaved populations from Idaho and Wyoming (sometimes referred to as *S. acutidens*) may be the result of further introgression from either *S. tridenticulatus* or *S. streptanthifolius* var. *borealis* (see Taxonomy section). Given this possibility it would be presumptuous to designate a hybrid formula for *rubricaulis* (*i.e., S. streptanthifolius* X *S. multilobatus*) because it may not be the result of hybridization between only two species.

On the other hand, when considered as a series of introgressants, the *rubricaulis* complex does not fit well into the species concept either. Since there is no evidence that introgression has ceased at the diploid level (the ranges of both parents are still sympatric), treating the introgressants as species may not accurately reflect the breeding relationships of the populations. Although the tetraploid populations of var. *rubricaulis* are probably genetically isolated from their diploid counterparts, the results of the numerical analysis indicate that they have not diverged structurally to any great degree so separating the tetraploids as a distinct species also, in this case, seems unwarranted.

Barkley (1968b) considers the *S. streptanthifolius* - *S. multilobatus* introgressants as belonging to two semi-distinct phases, the *uintahensis* phase which he associates with *S. multilobatus* and the *rubricaulis* phase which he associates with *S. streptanthifolius*. That this separation can be made and these alliances perceived, supports the current treatment of some of the introgressants as a variety of *S. streptanthifolius*.

The *rubricaulis* assemblage is an obvious problem group. Because its structure and flavonoid profile clearly ally it with *S. streptanthifolius*, it is treated here as a variety of *S. streptanthifolius*.

Although Barkley (1962), when he first recognized the *rubricaulis* phase, left it as part of *S. streptanthifolius* with no sub-specific or varietal ranking he treated *S. streptanthifolius* in a very broad sense. With the current more narrow treatment of *S. streptanthifolius*, the inclusion of var. *rubricaulis*, as simply part of *S. streptanthifolius*, would make the resulting species so variable that its relationship to var. *borealis*, *S. wallowensis* and *S. laetiflorus* would become much less clear.

In summary, the cladistic analysis of the *S. streptanthifolius* complex indicates the following:

1. *S. laetiflorus* most closely resembles the ancestral species in the *S. streptanthifolius* complex.
2. *Senecio streptanthifolius* separated first from the ancestral clade and it in turn, through separate speciation (hybridization) events, gave rise to *S. oodes* and *S. kluanei*.
3. More recently, through a similar hybridization event the taxon referred to as var. *rubricaulis* arose. *S. streptanthifolius* var. *rubricaulis* is considered to be a collection of introgressant populations between *S. streptanthifolius* and *S. multilobatus* with possible influence from other aureoid taxa.
4. Most recently, *S. streptanthifolius* gave rise to a northern narrow-leaved taxon, *S. streptanthifolius* var. *borealis*.

5. Finally, at some time between the origin of *S. streptanthifolius* and the present, the *S. laetiflorus* clade split producing *S. wallowensis*.

V. Phytogeography

The complex inter-specific relationships characteristic of the aureoid complex were most certainly forged, at least in part, by past geologic events and climatic changes. Both Barkley (1962) and Kowal (1975) presented brief synopses of the effects of post-glacial events upon distribution of the aureoid taxa that they studied. Barkley's discussion also included views on how the constantly changing patterns of overlap among species distribution, coupled with subsequent introgression, has contributed to the evolution of species within the group. The following discussion is similarly intended to present an overview of the historical events that have, in the author's opinion, shaped the *S. streptanthifolius* complex.

Barkley (1962) based his discussion on the assumption that the *Aurei* were reasonably well differentiated prior to the Wisconsin glaciation. This presumably valid assumption is supported by the overall distribution of the aureoid complex and much inferential information.

The current distribution and ecological preferences exhibited by many contemporary aureoid species, suggest that the group had its origin as part of a Tertiary assemblage of plants analagous to contemporary hardwood deciduous forests. This type of assemblage has in the past been envisioned as characterizing the large, circumpolar, homogenous Arcto-Tertiary Geoflora as described by Chaney (1947). More recently the Geoflora concept has been open to redefinition and refinement. Wolfe (1978) has shown that the plant assemblages that existed in Alaska during the Eocene do not conform to the Geoflora concept. Instead of using the floristic approach, Wolfe used the study of physiognomic leaf characters (*i.e.* margins, texture, apices) as a means of interpreting past climatic conditions. In this manner he concluded that the Eocene Alaskan floras contained a more tropical element than was predicted by the Geoflora model. Thus, it may be more correct to envision the aureoid senecios as having once been part of a Tertiary hardwood-deciduous assemblage, rather than members of the Arcto-Tertiary Geoflora (sensu Chaney). The paucity of aureoid species in Europe and Asia (Tutin *et. al.*, 1976; Komarov, 1961) furthers

this idea, suggesting that the aureoids were never circumboreal and that they originated somewhere in North America. According to Wolfe (1972) the Mixed Mesophytic Forests were not widely distributed in North America until the Miocene, when the exchange of warm temperate plants between Asia and North America via Beringia was reduced or had stopped. Conversely, the Miocene boreal forests are thought to have been Holarctic (Matthews, 1979), suggesting that a boreal origin for the aureoid senecios would have resulted in a greater species representation in contemporary Asian and European floras. Further evidence for the temperate, mesophytic affinities of aureoid senecios may be gleaned from their distribution patterns in Mexico and North America. The existence of aureoid species at high elevations in central Mexico is indicative of a pattern adhered to by other species or genera characteristic of the temperate mesophytic forest region (Daubenmire, 1978). The plants are thought to have migrated southward during the mid-Miocene and been subsequently cut off as sub-tropical arid zones expanded during the Pliocene. It should be noted that the disjunction referred to here applies only to the perennial species since, at present, the geographical gap has been somewhat reduced by the expansion in range of annuals, such as *S. imparipinnatus* Klatt., into areas of southwestern Texas and northeastern Mexico. The annuals are here postulated to have invaded these areas in post-Pliocene times.

The present distribution of aureoid species in North America can be effectively split into western and eastern assemblages with very few species extending across the south-central portions of the continent. Continental cooling combined with the emergence of a mid-continental arid region to effectively split the distributions of many mesophytic forest species as they migrated southward during the Miocene (Daubenmire, 1978). Subsequent divergence has resulted in both an eastern and a western centre of species diversity but no real east-west disjunction patterns within the species themselves. This east-west distribution pattern is nevertheless construed as evidence that aureoid senecios had evolved, at least to some degree, by the late Miocene.

The vegetation of southwestern North America also underwent a number of changes during the Miocene. Throughout this period more and more arid conditions prevailed, so that the more mesophytic vegetation was gradually supplanted in the drier lowlands by xerophytes. These xerophytes were considered by Axelrod (1958) to be part of the Madro-Tertiary Geoflora, an assemblage of semi-arid, chaparral, and semi-desert vegetation, thought to have originated in southwestern North America prior to the Miocene but with its greatest period of expansion during the Miocene and Pliocene.

The Pliocene was a period of continued or even greater aridity in western North America. The uplift of the Sierra Nevada and Cascade mountains created a rain-shadow over much of the Great Basin and eastern Oregon. In addition, block faulting plus uplifting throughout the Great Basin created the dissected basin and range topography of today. The drying trends present throughout the Pliocene are thought to have eliminated from the flora of western United States those eastern American elements which required summer moisture to survive (Holmgren, 1972). However, those mesophytic elements which could adapt to this arid environment might well be expected to exhibit some form of adaptive radiation as new niches left vacant by extinction became available. A genus containing a large number of species as *Senecio* does is apparently very capable of responding to niche availability, so it is during this time that the evolution of a number of aureoid species, currently inhabiting drier habitats in the southwest, is postulated to have occurred. Among others, the widespread and complex species, *S. multilobatus* and *S. neomexicanus*, may both have evolved from more mesophytic progenitors during this period.

By the beginning of the Pleistocene, the Great Basin flora was essentially the same as the present flora, with possibly some variation at the species level (Holmgren, 1972). This epoch was marked by cyclical warming and cooling trends, resulting in a series of glaciations. Since each subsequent glaciation eliminated much of the evidence for biogeographic events associated with the one before it, only evidence from the last Wisconsinan glaciation can be discussed in detail.

The four major glaciations are all thought to have had a similar effect on the vegetation since all four extended about the same distance south (Daubenmire, 1978). Plant species shifted temporarily to warmer latitudes and altitudes and then reinvaded vacant areas as the ice receded. As well as having a major effect on the distribution patterns of aureoid senecios in the north, glaciation, which occurred in many of the higher mountain ranges in the southwest, must have also affected the distribution of many southern aureoid species.

The major warming trend at the beginning of the Holocene also had major effects on plant distribution, the most obvious of which relates to the receding of the glaciers. In addition, because the warmer temperatures were not accompanied by a similar increase in precipitation, xerophytic vegetation expanded during this time. It is during this period that Barkley (1962) envisioned an eastern migration of western aureoid species along the front of the retreating glacier with concomitant introgression where eastern and western taxa met. A similar overlapping of species' ranges in the south probably occurred as the xerophytic species expanded into previously more mesic habitats.

In summary, the aureoid species in western North America are thought to have gone through a major diversification or speciation period during the Pliocene as aridity increased. Following that, the climatic changes associated with the Pleistocene glaciations and the succeeding hypsithermal, caused succesive range expansions and reductions in numerous aureoid species. The resulting introgression has sometimes led to the establishment of new species, occasionally of a polyploid nature.

The correlation of this historical information with the phylogeny of the *S. streptanthifolius* complex (as it is presented in the cladogram, Figure 9), allows the following inferences to be made.

The current distribution pattern of *S. streptanthifolius* var. *streptanthifolius* suggests that it was once widespread but has since had its southern range reduced such that it now occupies higher regions in the southwestern Rockies, the Sierra Nevada and some of the ranges between (*i.e.*, the Ruby and Jarbidge Mts. in Nevada). This range reduction is hypothesized to have occurred during

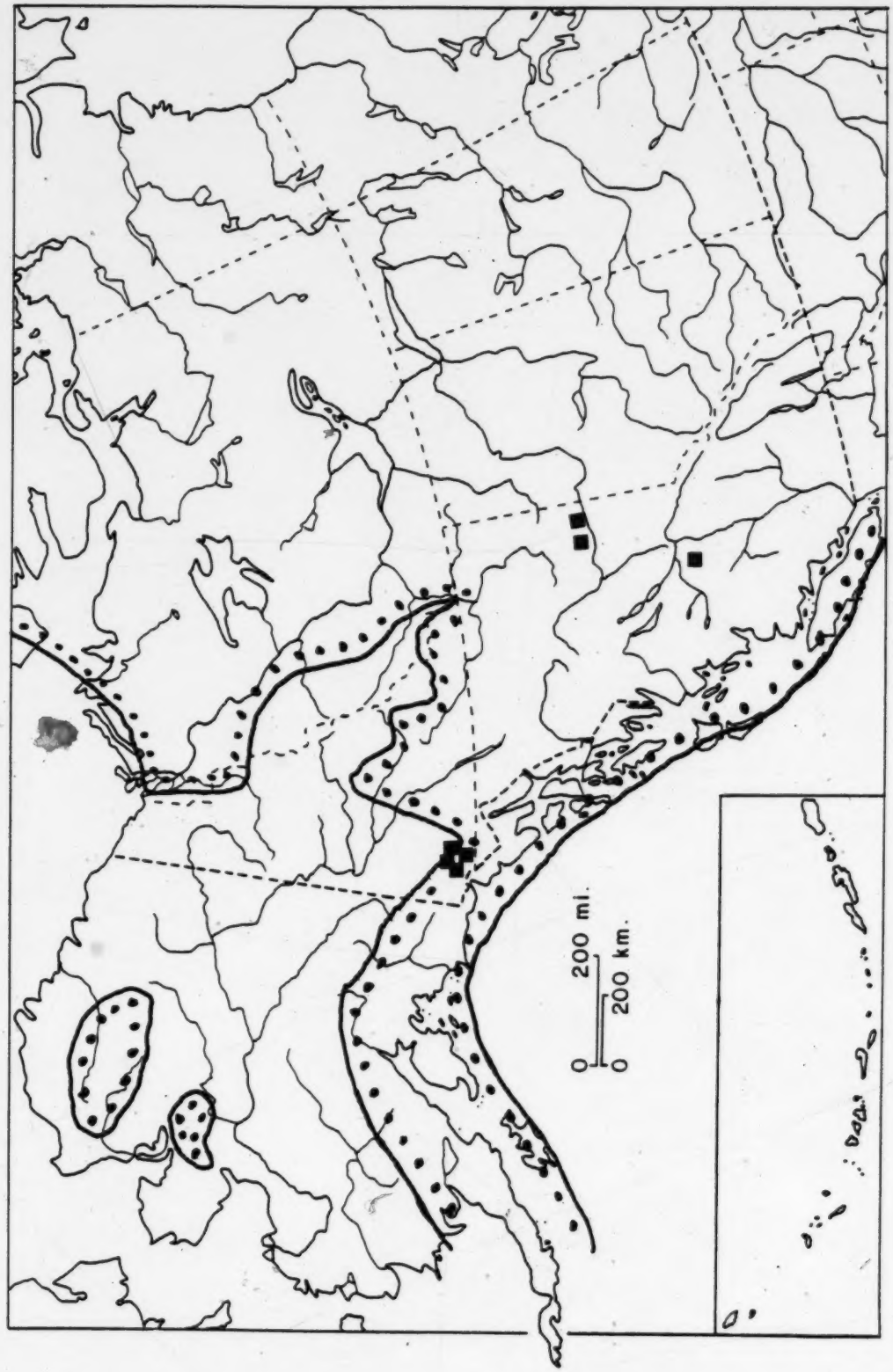
the late Pliocene with the onset of warmer and drier conditions especially in the rain shadow of the Sierra Nevada and the Cascades. The initial separation of the *S. streptanthifolius* clade from the ancestral clade therefore must have occurred sometime previously.

During the Pliocene, those more xerophytic species such as *S. neomexicanus*, *S. canus* and *S. multilobatus* also evolved in response to drier conditions. Introgression of these species with *S. streptanthifolius* occurred more recently, during the glaciations of the Pleistocene and the hypsithermal of the Holocene, as a result of range extension and overlap due to migration. During this time timberlines in the Great Basin have been estimated to have lowered by 600–1200 metres (Billings, 1977). *Senecio oodes*, *S. kluanei* and *S. streptanthifolius* var. *rubricaulis* are all thought to have arisen during the Pleistocene. *S. kluanei* however, has a very different range from the other two taxa. Its proximity to unglaciated areas in the Yukon suggests that its origin may be implicated more directly with continental Pleistocene glaciation. Displacement of taxa into or within unglaciated portions of Yukon Territory may have occurred with subsequent hybridization and polyploidy producing new taxa such as *S. kluanei*. The species has subsequently migrated to unglaciated areas as can be seen from the map in Fig. 10. The flavonoid results showed that *S. kluanei* and *S. streptanthifolius* var. *rubricaulis* share some similar compounds. This suggests that perhaps one of the now southern taxa had a more northern distribution prior to the Pleistocene and it was it rather than *S. streptanthifolius* var. *borealis* in more recent times that gave rise to *S. kluanei*. Finally, based on its distribution, the emergence of *S. streptanthifolius* var. *borealis* can be directly correlated with the onset of glacial retreat at the beginning of the Holocene. Hulten (1937) designates a number of species with this same distribution pattern as "continental western American radiants".

The origins of the last two species, *S. wallowensis* and *S. laetiflorus*, are more obscure. Besides sharing flavonoid characters, the two species have similar distributions. Both taxa are restricted to areas west of the Rocky Mountains, primarily in Oregon, and both extend only as far south as Mt. Rose,

Figure 10. Distribution of *Senecio kluanei* Bain in relation to the approximate maximum extent of Wisconsin glaciation in northwestern North America.

(Geol. Survey of Canada, 1968)


0 200 mi.
0 200 km.

Nevada. The speciation event resulting in the separation of these taxa likely occurred somewhere in the region currently occupied by the two species. Cooling temperatures during the Pliocene expanded alpine habitats in the Wallowa mountains and *S. wallowensis* may have evolved there via ecological isolation (sensu Stebbins, 1950) whereby peripheral populations in alpine or subalpine habitats gradually diverged from more ancestral types. In addition, it was during this period that the rising of the Cascades and the subsequent drying out of the interior of south-central Oregon and north-central California took place, causing the evaporation of previously existing bodies of water and the erosion of the lava beds covering the area. This created alkaline conditions and poor soil. It is in the more mesic alkaline meadows of this area that *S. laetiflorus* is found today, so it is assumed that *S. laetiflorus* was evolving in this region perhaps at the same time that *S. wallowensis* was evolving in response to cooling conditions at higher altitiudes. In either of the cases presented, the apparent disjunct distribution of *S. wallowensis* between the Wallowa Mountains and Mt. Rose, Nevada is difficult to explain because it is hard to envision a migration or dispersal mechanism which would result in establishment of populations on Mt. Rose yet not in the neighbouring Sierra Nevada. Axelrod (1956, 1957) was of the opinion that the largest of the volcanoes present in this area were able to support montane vegetation near their peaks during the late Miocene--early Pliocene whereas the Sierra Nevada had not reached a sufficient height to do so at this time. Thus, as long as one envisions a pre-Pliocene origin for *S. wallowensis*, its absence from the Sierra Nevada is easily explained. However, its absence from other early Pliocene montane regions (*i.e.*, volcanic peaks neighbouring the Wallowa Mountains in Idaho) then appears anomalous. An alternative explanation is that *S. wallowensis* became established in these two areas via long distance dispersal and that edaphic factors played a role in its establishment. Billings (1950) pointed out the importance of edaphic differences between the Sierra Nevada and the neighbouring Carson (including Mt. Rose) and Virginia ranges in determining the different floristic elements of the two ranges. Also the distribution of *S. laetiflorus* may in some way be shaped by edaphic

factors (Barkley, 1962). Further study may indeed show that edaphic factors control the distribution of *S. wallowensis*; for the present however, the fact that *S. wallowensis* occurs at both the southern and the northern extreme of *S. laetiflorus*' range is construed as evidence of a previous, more contiguous distribution for *S. wallowensis* and that both *S. laetiflorus* and *S. wallowensis* evolved at about the same time (early to mid-Pliocene) from a common ancestor whose range combined the current ranges of the two species.

VI. Taxonomy

Senecio Linnaeus, Sp. Pl. 2:866. 1753.

Annual, biennial or perennial herbs, shrubs or liana. Leaves alternate, cauline or basal, entire to deeply dissected. Inflorescence of one to many heads, commonly arranged in a loose corymbiform cyme. Heads radiate, rarely discoid, yellow or sometimes orange or reddish purple; involucre campanulate, turbinate or rarely cylindrical urceolate; principal bracts of the involucre equal in size and uniseriate, variable in number but with 13 or 21 being the most common, often subtended by a few reduced calyculate bracts; Ray flowers, when present, fertile, in a single row, variable in number, mostly 8 or 13, sometimes reduced; disc flowers perfect and fertile, the corolla slenderly tubular to abruptly expanded above into a campanulate 5-toothed limb; anthers obtuse to rounded or minutely tailed at the base; style branches semi-circular or elliptic-flattened in cross-section, truncate to rounded-obtuse, usually terminated by a small tuft of penicillate hairs. Achenes sub-terete, usually ribbed, glabrous, or hirtellous-pubescent especially along the angles. Pappus of numerous, white, barbellate setae.

Type species: *Senecio vulgaris* L.

Key to the species of the *S. streptanthifolius* complex

1a. Involucre pubescent, densely floccose-tomentose at the base often floccose-tomentose throughout; margins of the basal leaves evenly dentate to serrate for the whole perimeter of the leaf, not entire at the base. **2**

1b. Involucre glabrous, margins of the basal leaves either entire at the base, unevenly deeply dentate or lobate. **3**

2a. Leaf blades tomentose, obovate, ovate or occasionally widely ovate; leaf bases urneate or obtuse; Colorado, occasional in Wyoming and Nevada.

.....*S. oodes*

2b. Leaf blades glabrous, obovate to widely oblanceolate; leaf bases cuneate to narrowly cuneate; Yukon and northern British Columbia

.....*S. kluanei*

3a. Basal leaf bases obtuse, truncate or subcordate, blades widely ovate to orbicular; heads 3–7; alpine to sub–alpine, primarily of the Wallowa mountains and Mt. Rose, Nevada

.....*S. wallowensis*

3b. Basal leaf bases cuneate to attenuate or obtuse; blades ovate to oblanceolate or subspatulate; heads 6–20+; mesic, wooded slopes and meadows throughout western North America **4**

4a. Number of disc florets 45–85, heads large; leaves turgid and thickish, not obviously shiny or leathery in texture

.....*S. laetiflorus*

4b. Number of disc florets 25–45, heads small; leaves thick, shiny and leathery in texture

.....*S. streptanthifolius*

Senecio streptanthifolius Greene, Erythrea **3**:23. 1895.

Herbaceous perennial 2–4.5 dm tall, glabrous or occasionally with pubescence in the axils of leaves, or rarely very lightly floccose–tomentose on leaf surfaces, especially the lower surface or at bases of involucres; stems 1–3 arising from a single basal rosette; root of various types ranging from a taproot to a fibrous root, often giving rise to a stout branching caudex; basal leaves turgid and leathery in texture with petioles 2.5–7(–9) cm long, blades variable, oblanceolate to obovate to widely obovate, bases obtuse to cuneate, margins usually entire in the lower 2/3 of the blade, dentate or serrate dentate to crenate near the apex, occasionally deeply dissected in the lower portion with a prominent terminal lobe, 1.5–4(–5) cm long, 0.8–2.8(–3.5) cm wide; cauline leaves normally reduced, the lower ones resembling the basal leaves but usually more

dissected, the upper ones dissected or bract-like; inflorescence a loose corymbose cyme of (3-)8-20(-30) heads; involucral bracts 12-16(-21), (4-)4.5-7(-9) mm long; achenes glabrous; n = 23,46.

Senecio streptanthifolius, even though it is more strictly defined here, is still one of the more widespread aureoid senecios in western North America. It occupies a range of habitats from mesic to dry but is seldom found on poorly-drained sites. Typical *S. streptanthifolius* is easily recognized by its distinctly turgid, leathery, obovate leaves with mostly entire margins on the lower portions of the leaf. There is however, a wide array of structural variation from the typical. The assorted physical factors associated with different habitats, in combination with the introgressive influence of some sympatric aureoid species appear to be the major causes of this variation.

Three varieties have been recognized in the current study. The gradualness with which one variety intergrades with another poses a difficult problem for anyone wishing to present this variation coherently in a classification. However, it is clear that *S. streptanthifolius*, as it is currently defined, may be reliably divided into three more or less structurally distinct taxa, each of which exhibits some distributional integrity. A discussion of the relationships of these varieties to one another and to related species follows under each of the varietal headings.

Key to the varieties of *S. streptanthifolius*

1a. Basal leaf margins dissected, either lobate or deeply serrate-dentate; disc florets 6-7 mm long; cauline leaf margins lobate to pinnatisect ..... var. *rubricaulis*

1b. Basal leaf margins generally sub-entire, dentate to serrate-dentate at the apex; disc florets 4.5-6.0 mm long; cauline leaves usually sub-entire, often reduced and bract-like. **2**

2a. Leaf blades obovate to widely obovate, often twice as long as wide; western U.S., extending into southern British Columbia.

.....var. *streptanthifolius*

2b. Leaf blades oblanceolate to sub-spatulate, 2.5-3 times longer than wide; western and northern Canada, as far north as southern Yukon and Northwest Territories.

.....var. *borealis*

Senecio streptanthifolius Greene var. **streptanthifolius**.

Type: "on dry, wooded banks in Beaver Canyon, Idaho ... collected by the writer in August 1889 and distributed under the wrong name of *S. rapifolius*" *Greene s.n.* ND-G! (holotype), UC!, DH! Figure 11.

Senecio cymbalarioides var. *streptanthifolius* (Greene) Greenm., Ann. Missouri Bot. Gard. **3**:117. 1916.

Type: same as *S. streptanthifolius*.

Senecio cymbalarioides Nutt., Trans. Am. Phil. Soc. (II) **7**:412. 1841.

Type: "in Oregon". *Nuttall. s.n.* BM! (holotype).

Senecio adamsii Howell (*non* Cheeseman), Fl. N. W. Am. **1**:379. 1900.

Senecio suksdorfii Greenm., Bot. Gazette **53**:511. 1912.

Type: "by the base of cliffs, Mt. Adams Washington". *Howell s.n.* OSC! (isotype).

Senecio longipetiolatus Rydb., Bull. Torrey Bot. Club **27**:176. 1900.

Type: "Wyoming: Spread Creek, Teton Forest Reserve, 1897, *F.Tweedy 585* (type in the herbarium of N. Y. Botanical Garden)" NY! (holotype).

Senecio fulgens Rydb., Bull. Torrey Bot. Club **27**:177. 1900.

Senecio rydbergii A. Nelson in Coulter & Nelson Man.: 582. 1909.

Type: "Wyoming: Grand Creek, Teton Forest Reserve, 1897, *F.Tweedy 584* (type in the herbarium of N. Y. Botanical Garden)" NY! (holotype).

Figure 11. Holotype of *Senecio streptanthifolius* var. *streptanthifolius* Greene.

HERBARIUM
48040
GREENEANUM

IDAHO.

Senecio streptanthifolius Rydb.

Beaver Canon, Aug.

Rob. L. Greene, Journey of 1889.

Senecio subcuneatus Rydb., Bull. Torrey Bot. Club **27**:179. 1900.

Type: "Colorado: Grizzly Peak, 1896. *C.F.Baker s.n.* (type in the herbarium of N. Y. Botanical Garden)" NY! (holotype).

Senecio wardii Greene, Pittonia **4**:116. 1900.

Type: "collected somewhere in Utah in the year 1875, by L.F. Ward - in the US herbarium labelled *S. aureus* var. *alpinus* Gray." *Ward 332* taken to be the type. US! (holotype) MO! (isotype)

Senecio dileptiifolius Greene, Ottawa Nat. **15**:251. 1902.

Type: "Mr. Macoun's label for this bears the number 26,679 and indicated that the plant was collected 29 August at an altitude of 6000 feet" Chilliwack Valley, British Columbia. *Macoun 26,679* ND-G! (holotype), GH!, Photos F!, CAN!.

Senecio fraternus Piper, Contr. U.S. Nat'l. Herb. **11**:598. 1906.

Type: "Mt. Stuart, Kittatas Co., Washington, collected by *Sandberg & Leiberg 553*, July 24, 1893 at an altitude of 1060 m. The type specimen is in the U.S. Nat'l Herbarium numbered 285758" US! (holotype), F! MO! GH! UC!.

Senecio chapacencis Greene, Leaflets **2**:14. 1909.

Type: "Mt. Chapaca, in Okanogan Co., Washington at 4000' collected by *A.D.E. Elmer*, Aug., 1897. Collector's *n. 592*, as on sheet 352360 US Herb." US! (holotype).

Senecio aquariensis Greenm., Ann. Missouri Bot. Gard. **3**:144. 1916.

Type: "Utah: Aquarius Plateau, at 3050m., 5 Aug., 1875 *Ward 505*" MO! (holotype), GH!.

Senecio malmstenii Blake *ex* Tidestrom, Proc. Biol. Soc. Wash. **36**:183. 1923.

Type: "Little Podunk Creek, Kane Co., Utah *Malmsten 131*" US! (holotype), photo - NY!, GH!, MO!

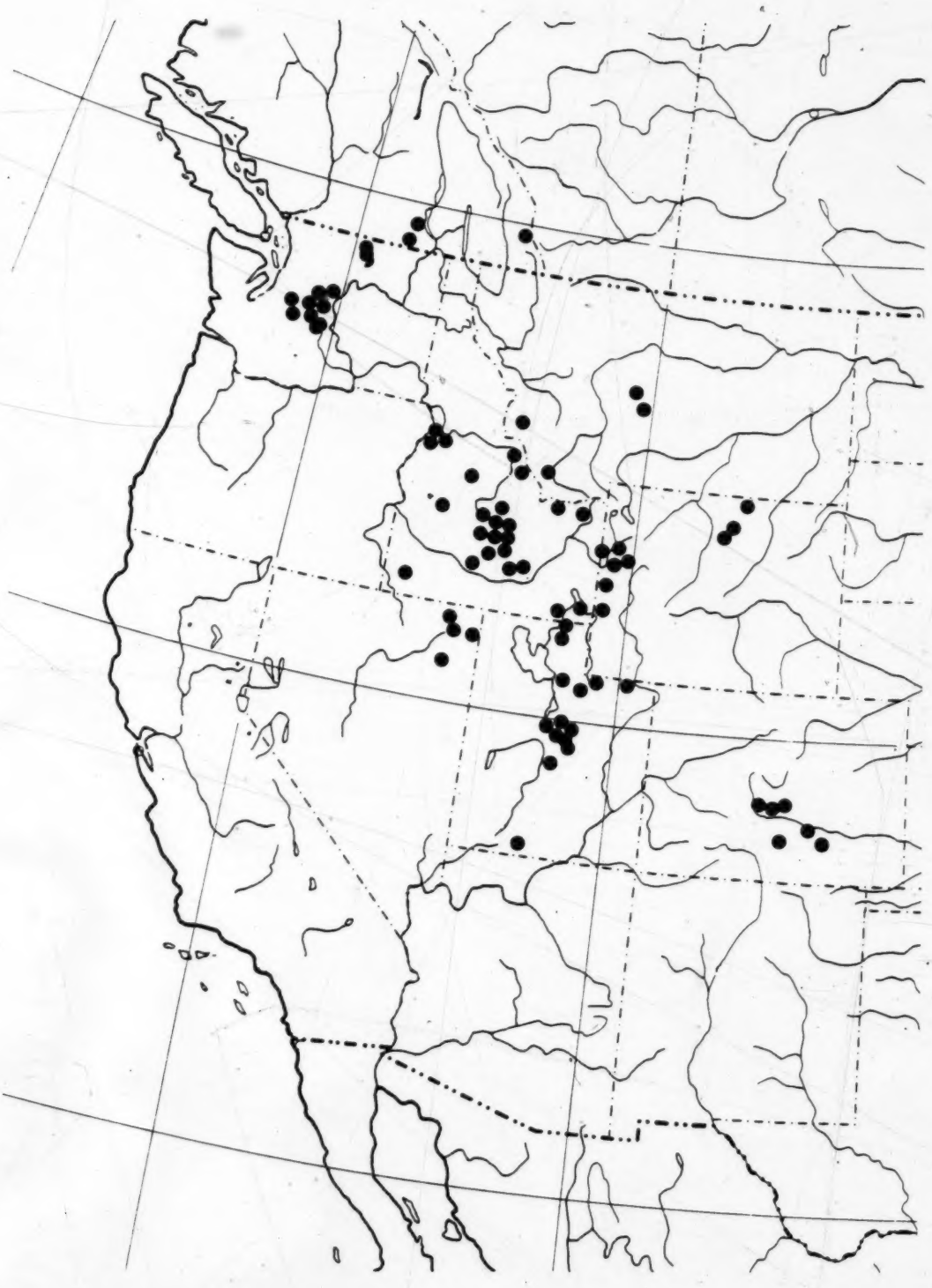
Leaf blades obovate to widely obovate, margins usually entire in the lower 1/2 to 2/3 of the blade, serrate-dentate to crenate near the apex, 2.5-4.0 cm long, (1-)1.3-2.8(-3.5) cm wide; petioles 3-7 cm long; flowering stalks 2.0-3.5

dm tall; cauline leaves reduced, subentire to lobate; n = 23,46.

DISTRIBUTION: wooded and open montane areas in northwestern United States, extending north into the interior of British Columbia and south into Utah, Colorado and with a few populations in California. Figure 12.

DISCUSSION: The typical variety of *S. streptanthifolius* exhibits a great degree of structural variation. In Washington, Oregon and southern British Columbia, var. *streptanthifolius* has obovate leaves with margins usually crenate rather than coarsely dentate. This form is most pronounced in the Wenatchee Mountains of Washington where collections have been identified as *S. suksdorfii* and *S. fraternus*. The collections of J. W. Thompson (#5831, #9502) represent this form well. It can easily be differentiated from *S. wallowensis* by its greater height, larger number of flower heads and less truncate leaf bases. It cannot, however, be easily separated from *S. streptanthifolius* and so *S. suksdorfii* (based on Howell, *s.n.*) and *S. fraternus* are considered to be synonyms. The specimen of *S. suksdorfii* from OSC cited by Barkley as an isotype has been examined. The holotype, if it exists, has not been found, however, since I have examined many specimens from the type locality, Mt. Adams, and none are *S. wallowensis*, I am confident that my separation of the Wallowa Mountains collections from this name is valid. Another specimen, from NY (Suksdorf *s.n.*), bears an annotation from Barkley that it is also an isotype, yet the two specimens are from different collections; they can't both be isotypes. Some of the confusion may arise from the fact that Greenman proposed *S. suksdorfii* as a *nomen. nov.* replacing *S. adamsi* Howell which is a later homonym. The new name, *S. suksdorfii*, is therefore associated with the old type (presumably Howell *s.n.*). The Suksdorf *s.n.* specimen (NY) is therefore rejected as an isotype. Since Barkley (1962,1978) does not ever cite this specimen as a type specimen, he has presumably reached the same conclusion. Piper (1906), in his original description of *S. fraternus*, indicates that it is intermediate between *S. adamsi* (*S. suksdorfii*) and *S. streptanthifolius* (*S.*

Figure 12. Distribution of *Senecio streptanthifolius* var. *streptanthifolius* Greene.



cymbalarioides Nutt.). I concur and feel that the three taxa are part of a continuum, but a continuum with a gap sufficient to allow the recognition of *S. wallowensis*. The type specimen for *S. chapacensis* also belongs in this continuum as does *S. dileptifolius*, albeit in a position much closer to *S. streptanthifolius*.

At the southern end of the distribution, the complications resulting from the close relationship between *S. neomexicanus* var. *mutabilis* and *S. streptanthifolius* make classification difficult. From limited field studies and extensive herbarium study I would agree with Barkley (1980) that introgression between these taxa (most notably in southeastern Utah but also in southern Colorado) provides a continuum of variation. The results of the numerical analysis support this in as much as *S. neomexicanus* was the only species outside the *S. streptanthifolius* complex to cluster with *S. streptanthifolius*. Flavonoid analysis also reflects a close relationship. *Senecio neomexicanus* var. *mutabilis* could probably as easily be treated as a tomentose variety of *S. streptanthifolius*, however, since this would not clarify problems in either *S. streptanthifolius* or *S. neomexicanus* and because leaf pubescence is relatively useful for characterizing *S. neomexicanus*, var. *mutabilis* is best left as part of *S. neomexicanus*. The type specimen of *S. cognatus* Greene, which Barkley put in synonymy with *S. streptanthifolius*, is here removed and placed in synonymy with *S. neomexicanus* var. *mutabilis*. The relationship of *S. oodes* to *S. neomexicanus* will be discussed later.

The relationship of *S. tridenticulatus* to *S. streptanthifolius* is not clearly elucidated by this study. Only two collections of *S. tridenticulatus* were made in Colorado where the ranges of the species overlap. *Senecio tridenticulatus* is predominantly a species of the plains so that introgression is only a problem in a relatively small portion of its range. Flavonoid profiles were once again too similar to those of *S. streptanthifolius* to be very informative. Given that the two have the same chromosome numbers and occupy similar habitats in their areas of overlap, hybridization is to be expected. The type specimen of *S. subcuneatus* Rydb. exhibits *S. tridenticulatus* characters in its leaf shape and may

represent just such a hybrid. Confusion arises when trying to separate *S. streptanthifolius* var. *borealis* from *S. tridenticulatus*. Barkley (1978) treats the populations of var. *borealis* from the Great Slave Lake area of Northwest Territories as disjunct populations of *S. tridenticulatus* where in fact they fit very easily into var. *borealis*. They grow in very dry, sandy pine stands, are somewhat smaller and have narrower leaves than the more southern Rocky Mountain populations. When these extreme populations are compared to typical *S. streptanthifolius* they appear out of place, but when treated as part of the narrow-leaved var. *borealis*, they fit well.

Senecio pauperculus is also reported to intergrade with var. *streptanthifolius* (Barkley, 1962,1978). Although flavonoid profiles once again do not aid in elucidating this introgression, specimens that are structurally intermediate do occur. The evenly crenate-dentate margins of *S. pauperculus* can usually be used to advantage in separating the two taxa. Leathery leaf texture, usually considered a *S. streptanthifolius* character, is also present in *S. pauperculus* populations and so is less reliable.

Senecio streptanthifolius var. **borealis** (T. & G.) J. F. Bain, *comb. nov.*

Basionym: *Senecio aureus* var. *borealis* Torrey & Gray, Fl. N. Am. **2**:442. 1843.

Senecio cymbalarioides var. *borealis* (T. & G.) Greenm., Ann. Missouri Bot. Gard. **3**:117. 1916.

Type: "partly Hook.,! *l.c.*" between N.Y. & E. -- *Dr.* (presumably Drummond) *s.n.* GH! (lectotype). Figure 13.

Leaf blades oblanceolate to subspatulate, margins entire except for the apex which is dentate usually with 3-7 teeth, cuneate at the base, 1.5-2.5 cm long, 0.8-1.4 cm wide; petioles 2.5-3.5 cm long; flowering stalks 2.0-3.5 dm

Figure 13. Lectotype of *Senecio streptanthifolius* var. *borealis* (T. & G.) Bain (specimen on the right)

Herbier des Missions
OBLATS DE MARIE IMMACULÉE
VICARIAT DE S. E. MGR BREYNAT, O. M. I.
MACKENZIE CANADA
Senecio cymbalarioides Nutt.,
var. arcticus (T. & G.) Fernald
Providence
REMARQUES: 1ère croisière missionnaire du "Guy"
Herborisateur: Père A. Dubay, O.M.I.
HARVARD
Senecio streptanthifolius Fern.
Senecio cymbalarioides Nutt.,
var. arcticus (T. & G.) Fernald
DET. BY J. M. GREENMAN
75
SYN. FL. N. AMER.
Tres. & Gray, Flora, N. Amer.
Arctic Am.

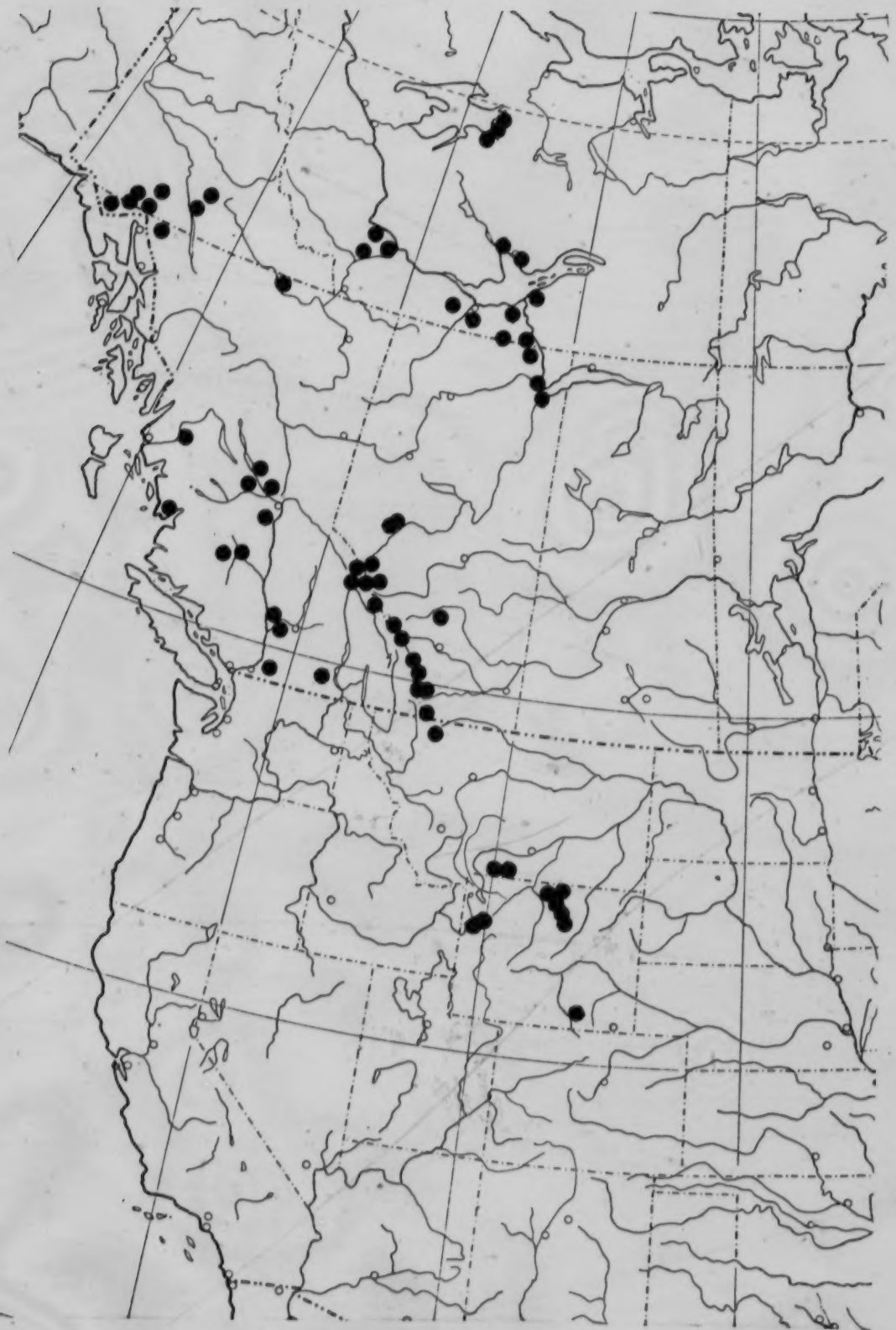
tall; cauline leaves usually very reduced, entire to subentire and bract-like; n = 23.

DISTRIBUTION: on well-drained, open woodland sites in the Rocky Mtns. and the surrounding Boreal Forest region from Yukon and Northwest Territories south to Montana and Wyoming on the eastern side of the Rocky Mountains while only extending into southern British Columbia on the western side. Figure 14.

DISCUSSION: The northern populations of *S. streptanthifolius*, here segregated as var. *borealis*, all have distinctly oblanceolate leaves with mostly entire margins. Their habitats are fairly uniform as they are most often found on open, sandy or well-drained sites in *Pinus contorta* stands. Typical var. *streptanthifolius* takes over from var. *borealis* in southern British Columbia and generally in Montana. However farther east, the southern limit of var. *borealis* extends into Wyoming where it has been well collected in the Bighorn Mountains.

Senecio streptanthifolius var. *borealis* is structurally much less variable than var. *streptanthifolius*. Although *S. streptanthifolius* (*s.l.*) is thought to introgress with two wide ranging species (*S. pauperculus* and *S. canus l.c.* Barkley, 1978) which are sympatric with var. *borealis*, both these species are polyploid within this area of sympatry while var. *borealis* is diploid. Only one collection of tetraploid var. *borealis* was made (Bain 057) from central British Columbia. This population was growing within fifty metres of typical diploid var. *borealis* and typical tetraploid *S. pauperculus*. Although it may represent a hybrid between these two taxa it seems unlikely that the *S. pauperculus* parent came from the tetraploid population. I can only hypothesize the existence of a diploid *S. pauperculus* parent somewhere in the vicinity. After examination of the voucher specimen (M-4754, UC) for the reported hybrid *S. canus* X *S. streptanthifolius* (Ornduff *et. al*, 1967) I feel it is a specimen of *S. canus*. I have found no hybrid specimens of *S. canus* and *S. streptanthifolius* var. *borealis* although I have seen specimens of *S. canus* in the foothills of Alberta which are nearly

Figure 14. Distribution of *Senecio streptanthifolius* var. *borealis* (T. & G.) Bain



glabrous.

Senecio streptanthifolius var. *borealis* is separated as a variety because, for most of its range, it is easily distinguishable from typical *S. streptanthifolius* although chemically and structurally the two are closely related. I believe that two factors have contributed largely to the differentiation of var. *borealis*. Firstly var. *borealis* is derived from a relatively small, homogeneous proportion of the *S. streptanthifolius* complex, that which was located near the edge of the last glacial advance. Secondly, in its migration into the new territory left open after glaciation, it was not accompanied by other diploid aureoid species (*S. canus* and *S. pauperculus* are tetraploid) so that it was and remains relatively free of the introgressive pressures that the southern diploid species exert on one another and in this manner remains distinct from other species and from var. *streptanthifolius*.

The designation of a lectotype for var. *borealis* was necessitated by Torrey and Gray's failure to typify *S. aureus* var. *borealis* in the original description. Torrey and Gray (1843) made two citations in the following order:

"... *S. aureus*, partly, Hook.! l.c.;

S. cymbalariodes, Nutt.! in Trans. Amer. Phil. Soc. l.c. p. 412 ... "

From this it is clear that Torrey and Gray included *S. cymbalariodes* Nutt. as part of *S. aureus* var. *borealis*, just the opposite of what is proposed here. Without specimens to refer to however, it is difficult to ascertain the grounds upon which Torrey and Gray based their taxon. Greenman (1916) transferred *S. aureus* var. *borealis* to varietal status under *S. cymbalarioides* Nutt. but did not lectotypify the taxon. The first specimen he cited, however, was considered by Greenman to be one of Hooker's collections (at GH) from Arctic America. The specimen was in fact not collected by Hooker but was annotated as having been included in the Flora Boreali-Americana. The collector was most likely Drummond as the label bears a distinct 'Dr' but no other collector's name (see Figure 13). This specimen had been previously annotated by Torrey and Gray for the *Flora of North America* (1843) as *S. aureus* var. *borealis*. Conversely, the specimen

(at GH) of *S. cymbalarioides* collected by Nuttall from the "Rocky Mountains", bears no annotation label from Torrey and Gray; nor do the Nuttall collections of *S. cymbalarioides* at BM (holotype) or at PH. Thus the Hooker specimen cited by Greenman (at GH) is the only one which can be reliably associated with both the citations given by Torrey and Gray (1843) and with their own description (*l.c.* p. 443). It is therefore chosen as the lectotype for *S. aureus* var. *borealis* T. & G.

Senecio streptanthifolius var. **rubricaulis** (Greene) J. F. Bain, *comb. nov.*

Basionym: *Senecio rubricaulis* Greene, Pittonia **3**:89. 1896.

Type: "foothills of the Clover Mtns., Nevada, 1893; found by the author" *Greene s.n.* ND-G! Figure 15.

Senecio acutidens Rydb., Bull. Torrey Bot. Club **27**:180. 1900.

Type: "Union Pass, Wyoming. *A. Nelson 858* (type in the herbarium of N. Y. Botanical Garden)" NY (holotype, not seen) RM! MO! US.

Senecio jonesii Rydb., Bull. Torrey Bot. Club **27**:179. 1900.

Type: "Utah: Alta, Wasatch Mountains, 1879, *M.E. Jones 1125* (type in Columbia herbarium)" NY! (holotype).

Senecio platylobus Rydb., Bull. Torrey Bot. Club **27**:181. 1900.

Type: "Utah: Wasatch Mtns., 1869, *Watson 671* (type in the Torrey herbarium)" NY! (holotype) US! GH!.

Senecio pammelii Greenm., Ann. Missouri Bot. Gard. **3**:118. 1916.

Type: "Utah: moist, rocks and shady woods, Peterson Canyon, Peterson, alt. 2895 m., 19 July, 1902 *Pammel & Blackwood 3870* (Mo. Bot. Gard. Herb.)" MO! (holotype).

Figure 15. Holotype of *Senecio streptanthifolius* var. *rubricaulis* (Greene) Bain

UNIV. OF NOTRE DAME
GREENE HERBARIUM
NDG 063310
POST 1906 NUMBER SERIES
CANADIAN LABORATORY SUPPLIES
LIMITED
HERBARIUM OF KANSAS STATE UNIVERSITY
MANHATTAN, KANSAS
SENECIO rubricaulis Greene, Pittonia 3:39. 1896.
HOLOTYPE
Annotated by T. M. Barkley
1973
HERBARIUM
47647
GREENEANUM
HERB. UNIVERSITY OF CALIFORNIA
Senecio rubricaulis, Greene.
Clover Mts., Nevada

Senecio rubricaulis var. *aphanactis* Greenm., Ann. Missouri Bot. Gard. **3**:174. 1916.

Senecio cymbalarioides var. *aphanactis* (Greenm.) Blake in Tidestrom, Contr. U.S. Nat'l. Herb. **25**:614. 1925.

Type: Utah: dry canyon, Logan, Cache Co., alt. 1525m., 23 June, 1910 *C.P. Smith 2208* (Field Mus. Herb., photograph in Mo. Bot. Gard. Herb.)' F! (holotype) UTC photo-MO (not seen).

Leaf blades obovate to ovate, deeply dentate or serrate to lobate, 2.5-4.5(-7.0) cm long, 1.5-2.8 cm wide; petioles 3-8 cm long; flowering stalks 3-4.5 dm tall; cauline leaves usually lobate to pinnatifid; n = 23, 46.

DISTRIBUTION: open, dry sites and woodlands, primarily in the mountain ranges of the Great Basin region but occasionally found in Colorado and the Sierra Nevada range in California. Figure 16.

DISCUSSION: *Senecio streptanthifolius* and *S. multilobatus* are sympatric in parts of the Wasatch and Uinta Mountains in Utah and Wyoming. On these drier sites, the basal leaves of *S. streptanthifolius* are often more coarsely dentate, even lobate, than are the leaves of typical var. *streptanthifolius*. These populations are all referred to var. *rubricaulis* in this treatment. Barkley (1962) previously referred to this as the *rubricaulis* phase and suggested that it resulted from the introgression of *S. streptanthifolius* and *S. multilobatus*. Morphology supports this idea but flavonoid profiles give no evidence one way or the other. The profiles of all three taxa are very similar and no evidence of complementation exists in the *rubricaulis* profile.

Polyploidy has also played a role in adding to the variability present in var. *rubricaulis*. The taller more robust specimens from more mesic sites in the Wasatch Mountains, previously referred to as *S. platylobus* (Rydberg, 1900; Greenman, 1916), are apparently tetraploid based on counts presented in this

Figure 16. Distribution of *Senecio streptanthifolius* var. *rubricaulis* (Greene) Bain

study. Flavonoid profiles, however, do not support the separation of this race from the rest of var. *rubricaulis*. Then too, tetraploid populations have been found farther north (*e.g.* Bain 107) which do not always show the same degree of leaf dissection as do the *platylobus* specimens. These specimens resemble what has been called *S. acutidens* Rydb. in the past. Diploid populations have also been found (*e.g.* Bain 108) fitting this description. Their coarsely dentate leaves and taproot appear distinctive when compared with typical var. *streptanthifolius* but, when associated with *rubricaulis* and *platylobus*, the three entities unite in a heterogeneous assemblage. When trying to associate these entities with a type specimen some problems occur. Fortunately no problem exists for the type specimen of *S. rubricaulis*. Greene's specimen (ND-G) from Nevada appears typical. It is somewhat larger than average and so may possibly be a tetraploid, however, if later studies suggested that is a tetraploid specimen that would only create a problem if the tetraploids were separated from the rest of var. *rubricaulis*. On the other hand, while one isotype of *S. acutidens* examined (Nelson 858, RM) appears to me to be typical var. *streptanthifolius* and not *S. tridenticulatus* as indicated by Barkley (1978), another isotype (MO) has the more typical dentate leaves and fits well into var. *rubricaulis*. The placing of the name in synonymy with var. *rubricaulis* is thus somewhat provisional until the holotype (NY) is examined. The placement of the name does not, however, affect the treatment of the specimens which would in any event remain part of var. *rubricaulis*. A similar problem relating to the heterogeneity of a type collection is encountered with *S. platylobus*. Although the holotype of *S. platylobus* (Watson 671, NY) fits the original description, isotypes (GH and US) are not nearly as easily identified as *S. platylobus*. This problem was also encountered and elucidated by Greenman (1916).

The other related taxon or phase as outlined by Barkley (1968b) is *S. uintahensis* which is more closely related to *S. multilobatus* than it is to *S. streptanthifolius*. Although Barkley (l.c.: 279) characterizes the phase as having leaves with rounded lateral lobes, the character is present but not pronounced in the holotype (Nelson 4511, RM) and isotype (NY) examined. Greenman separates

S. uintahensis from *S. multilobatus* by the former's glabrous achenes while Ornduff *et. al.* (1967) maintain *S. uintahensis* as separate based on its different chromosome number (n=46 vs. n=23 for *S. multilobatus*). Problems associated with *S. uintahensis* can only be solved through a thorough study of the *S. multilobatus* complex, a task which is beyond the scope of this study. What is clear from this study is that the apparent introgression occurring between *S. streptanthifolius* and *S. multilobatus* occurs at two ploidy levels. At the diploid level the *rubricaulis* phase encompasses many of the introgressants while at the tetraploid level, it is the *platylobus* and *uintahensis* phases which are apparently the results of introgression. In addition, the *S. acutidens* specimens, both diploid and tetraploid, may be the results of introgression but they are much more similar to *S. streptanthifolius* than to *S. multilobatus*. As well as this suggested relationship to *S. multilobatus*, a possible relationship of *S. acutidens* to *S. tridenticulatus* (Barkley, 1978) has also already been mentioned. This latter relationship may actually be a relationship to *S. streptanthifolius* var. *borealis*. The structural similarity of the latter taxon and *S. tridenticulatus* has already been noted.

The close interrelationship of these taxa at different ploidy levels does not allow for easy separation of the different structural types present. Separation of the three entities -- *acutidens, platylobus,* and *rubricaulis* -- into a separate variety, var. *rubricaulis*, is done here based on morphology. Variety *rubricaulis* still encompasses a high degree of structural heterogeneity which in part, relates to its two ploidy levels. Further study may eventually result in more separation based on chromosome number.

Senecio oodes Rydberg, Bull. Torrey Bot. Club **33**:158. 1906.

Type: "Colorado: Mt. Harvard, 1896, *F.E. Clements 39* (type)" NY! (holotype). Figure 17.

Senecio leonardii Rydb., Bull. Torrey Bot. Club **37**:468. 1910.

Type: "Utah: near divide, head of American Fork Canyon, July 29, 1885, *Leonard 143* (type in herbarium of N. Y. Botanical Garden)" NY! (holotype).

Herbaceous perennial 3–4 dm tall, loosely floccose–tomentose especially in the leaf axils and at the bases of the involucres; stems 1–3, arising from a short but prominent rootstock, basal leaves floccose–tomentose, occasionally glabrate with age, petiole stout, 2.5–7(–9) cm long, leaf blades obovate to ovate or occasionally widely ovate, cuneate or sometimes obtuse at the base, margins evenly serrate to crenate, 3–4 cm long, 1.5–2.7 cm wide; cauline leaves few, reduced upward, the lower ones resembling the basal leaves but often more oblanceolate and more dissected, the upper ones usually greatly reduced and entire; inflorescence a corymbose cyme of 6–13 woolly heads; involucre often dark in colour; involucral bracts 12–20, 4–5.5 mm long, tomentose at least at the base; achenes glabrous; n = 23.

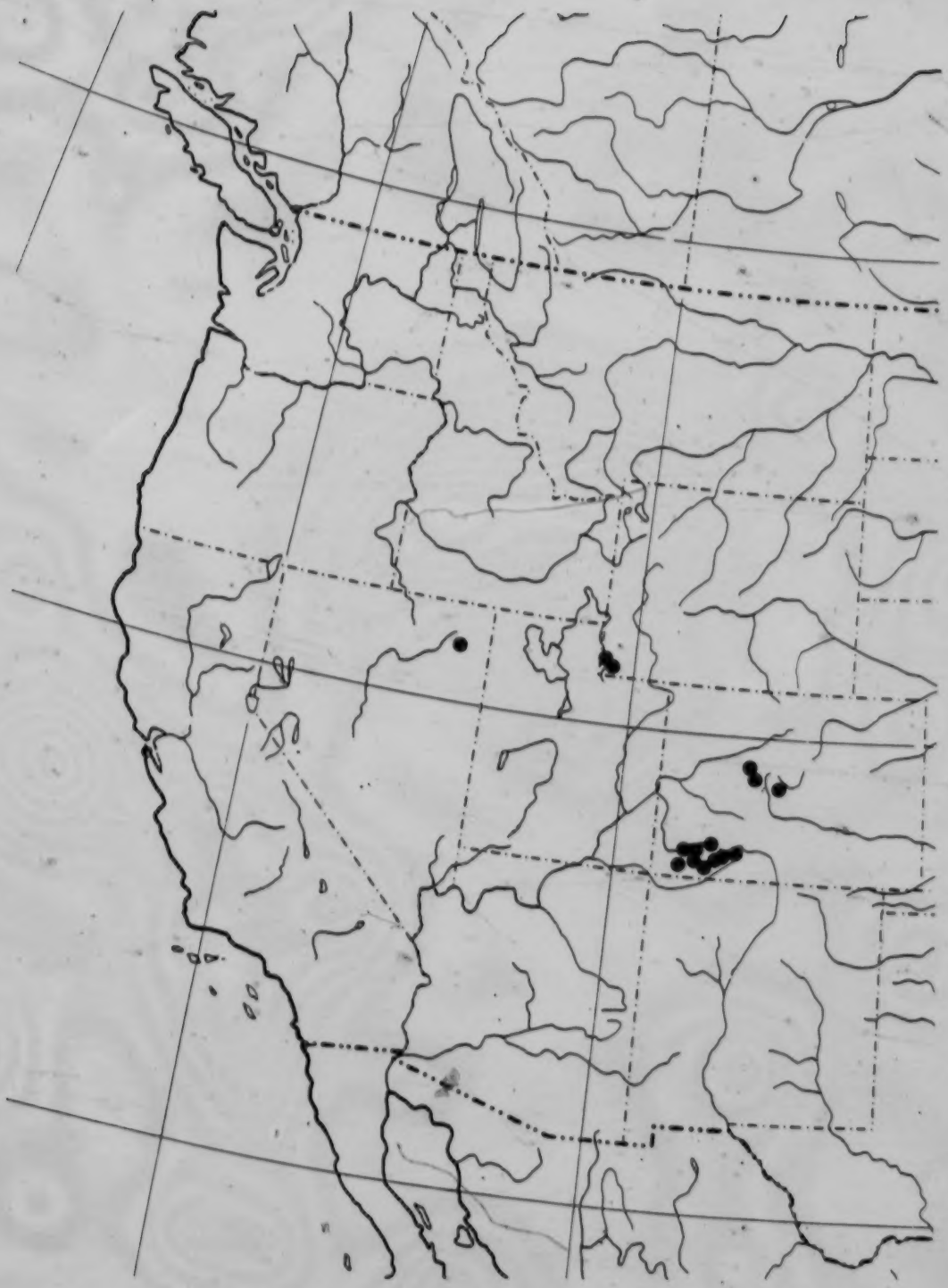
DISTRIBUTION: disturbed open sites at higher elevations in southwestern and central Colorado (Lake, Eagle and Summit Counties); also Wyoming and neighbouring Utah as well as Elko Co., Nevada. Figure 18.

DISCUSSION: The present circumscription of *S. oodes* includes both the *leonardii* phase and *molinarius* phase as outlined by Barkley in 1962. In his

Figure 17. Holotype of *Senecio oodes* Rydberg

NEW YORK
BOTANICAL
GARDEN
HERBARIUM OF
THE NEW YORK BOTANICAL GARDEN
Senecio rodeo Rydb.
Mt. Howard, Oct. 1896.
Type

Figure 18. Distribution of *Senecio oodes* Rydberg



1978 treatment, Barkley placed *S. molinarius* in synonymy with *S. wernaerifolius* where, judging from the type specimen (GH), it belongs. However, Barkley's clear designation of the Bethel, Willey, Clokey specimen (#4391) as representative, leaves little doubt about what he envisioned as the *molinarius* phase. He separated the two phases largely on the amount of pubescence present. The type specimen of *S. leonardii* Rydb. (Leonard 143, NY) was judged sufficiently similar to the Bethel, Willey, Clokey specimen to warrant the combining of the two phases. Subsequent structural, chemical, and chromosomal analyses all supported the joining of these taxa. In addition, the examination of the type of *S. oodes* Rydb. revealed it to be part of this taxon and since *S. oodes* predates *S. leonardii* it is the legitimate name. As with other aureoid species, *S. oodes* embodies some degree of variation so it is perhaps unfortunate that the type specimen of *S. oodes* is less distinctive than that of *S. leonardii*. The loosely floccose, thick leaves with crenate margins are visible on both specimens as are the basally slightly villous to floccose involucres. The variation in the amount of tomentum present on the leaves of *S. oodes* makes the examination of the other characters necessary for accurate identification. Even so, difficulty sometimes arises in separating *S. neomexicanus* var. *mutabilis* from *S. oodes* in southwestern Colorado. *Senecio oodes* has generally wider leaves with a smaller leaf/petiole length ratio and more regularly toothed margins. In addition, Greenman separates the two taxa (*S. leonardii* and *S. mutabilis sensu* Greenman) on the basis of *S. oodes* having glabrous achenes (a trait also ascribed to *S. oodes* by Rydberg) while *S. mutabilis* has hirtellous achenes. Flavonoid profiles clearly separate *S. oodes* and *S. mutabilis* while the shared presence of isorhamnetin 3/7 glycosides between *S. canus* and *S. oodes* suggests that *S. oodes* may be more closely related to *S. canus* than to *S. neomexicanus* var. *mutabilis*.

Senecio laetiflorus Greene, Pittonia 3:88. 1896.

Type: "the type specimens collected by myself in July last, near Boca, California." *Greene s.n.* ND-G! (holotype). Figure 19.

Herbaceous perennial, 3-5(-6) dm tall, glabrous or occasionally very lightly tomentose; stems 1-3, arising from a fibrous rootstock; basal leaves petiolate, petioles (4-)5-9(-11) cm long, leaf blades ovate to obovate or elliptic, tapering at the base, margins serrulate or crenate to subentire or occasionally deeply dissected, 2.5-7(-10) cm long, 1.5-3.5 cm wide; cauline leaves few and reduced, lower ones deeply dissected and often clasping at the base, the upper ones either deeply dissected or subentire and bract-like; inflorescence a loose corymbose cyme of (3-)6-12(-14) heads; involucre glabrous, bracts 16-22, 4-6 mm long; achenes glabrous; n = 23.

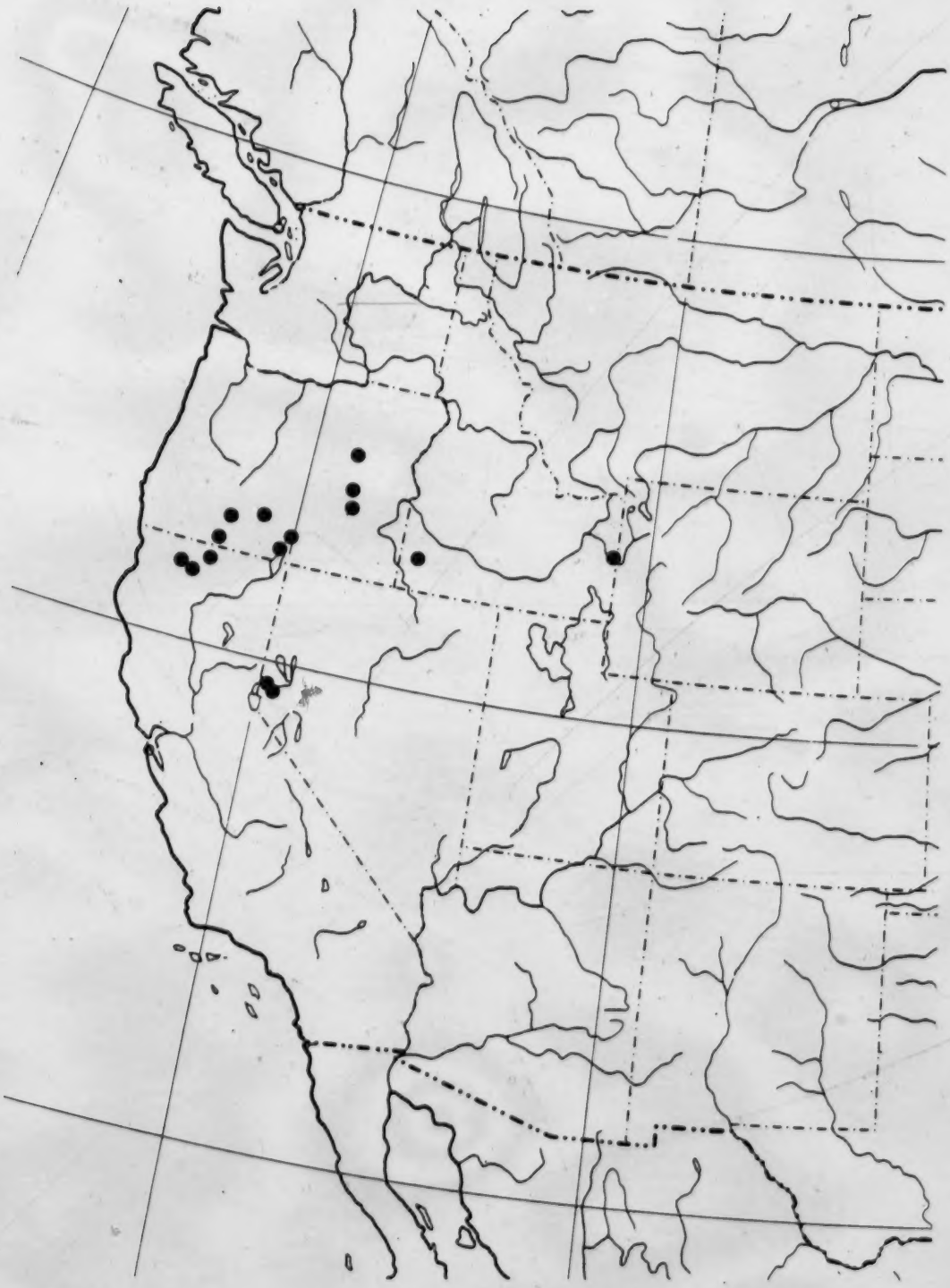
DISTRIBUTION: open mesic sites in eastern and southern Oregon and adjacent northern California. Figure 20.

DISCUSSION: *Senecio laetiflorus* is unusual in the *S. streptanthifolius* complex in that its habitat is not predominantly well drained sites in the boreal or montane forests but rather the damp alkali meadows of eastern Oregon and northeastern California. This apparent affinity for more mesic sites allies *S. laetiflorus* with the wide ranging related species, *S. pauperculus* and *S. pseudaureus* as well as the more restricted *S. debilis*. *Senecio laetiflorus* also resembles *S. pauperculus* in a number of structural features including height, cauline leaf dissection and head number, but differs in that its leaves often have entire margins and a fleshier texture, although not as leathery a leaf texture as in *S. streptanthifolius*. The fact that *S. pseudaureus* in northwestern North America has a chromosome number of n = 20,40 indicates that any alliance with *S. laetiflorus* may be superficial.

Figure 19. Holotype of *Senecio laetiflorus* Greene

063158
HERBARIUM
47707
GREENEANUM
HERBARIUM OF KANSAS STATE UNIVERSITY
MANHATTAN, KANSAS
1973
HOLOTYPE
Annotated by T. M. Barkley
PLANTS OF CALIFORNIA
Senecio latiflorus, Jeanne
Boca, 26 July

Figure 20. Distribution of *Senecio laetiflorus* Greene



Senecio wallowensis *sp. nov.*

Type: Ice Lake, Wallowa mountains, Oregon. *Bain 199* ALTA (holotype). Figure 21.

Herbaceous perennial, 0.9–1.9(–2.5) dm tall, glabrous; stems 1 or occcasionally 2–3 when arising from a terminally branching caudex; basal leaves petiolate, the petioles 1.5–3.5 cm long, blades widely or very widely ovate to circular, obtuse or truncate to weakly cordate at the base, margins serrate or dentate to crenate, 1.1–1.9 cm long, 1.1–1.8 cm wide; cauline leaves 2–4, bract–like or occasionally dissected; inflorescence a congested corymbose cyme of 3–7 heads; involucre glabrous, involucral bracts 15–21, 4.5–5.5 mm long; achenes glabrous; n = 23.

DISTRIBUTION: High alpine and sub–alpine sites in the Wallowa Mts. in Oregon, Washoe Co. in western Nevada and on Mt. Ranier in the Cascade Mts. Figure 22.

DISCUSSION: *Senecio wallowensis* is a small sub–caespitose entity which is restricted to open alpine and subalpine slopes most commonly in Nevada and Oregon. I define this taxon in a much more restrictive manner than does Greenman (1912). Greenman referred six collections to *S. suksdorfii* when he published the name change from *S. adamsii* Howell. Of these, only two (Cusick 3131, Heller 9896) are *S. wallowensis*. The other four (Henderson 2309, Suksdorf *s.n.*, Brandegee 915 Tarleton, 62) are *S. streptanthifolius*.

The restricted distribution of *S. wallowensis* may be indicative of the relictual nature of the species. It is known from only three locations in western North America and in no case is it known to occur sympatrically with other species in the complex. It does however, in one instance occur in the vicinity of another rare aureoid species, *S. porteri*. Both are reported to occur in the Wallowa mountains. Although *S. wallowensis* has been collected repeatedly over the years in this region, *S. porteri* has apparently been collected once (Cusick

Figure 21. Holotype of *Senecio wallowensis* Bain

HERBARIUM - THE UNIVERSITY OF ALBERTA

FLORA OF OREGON

Senecio wallowensis Bain n. sp.

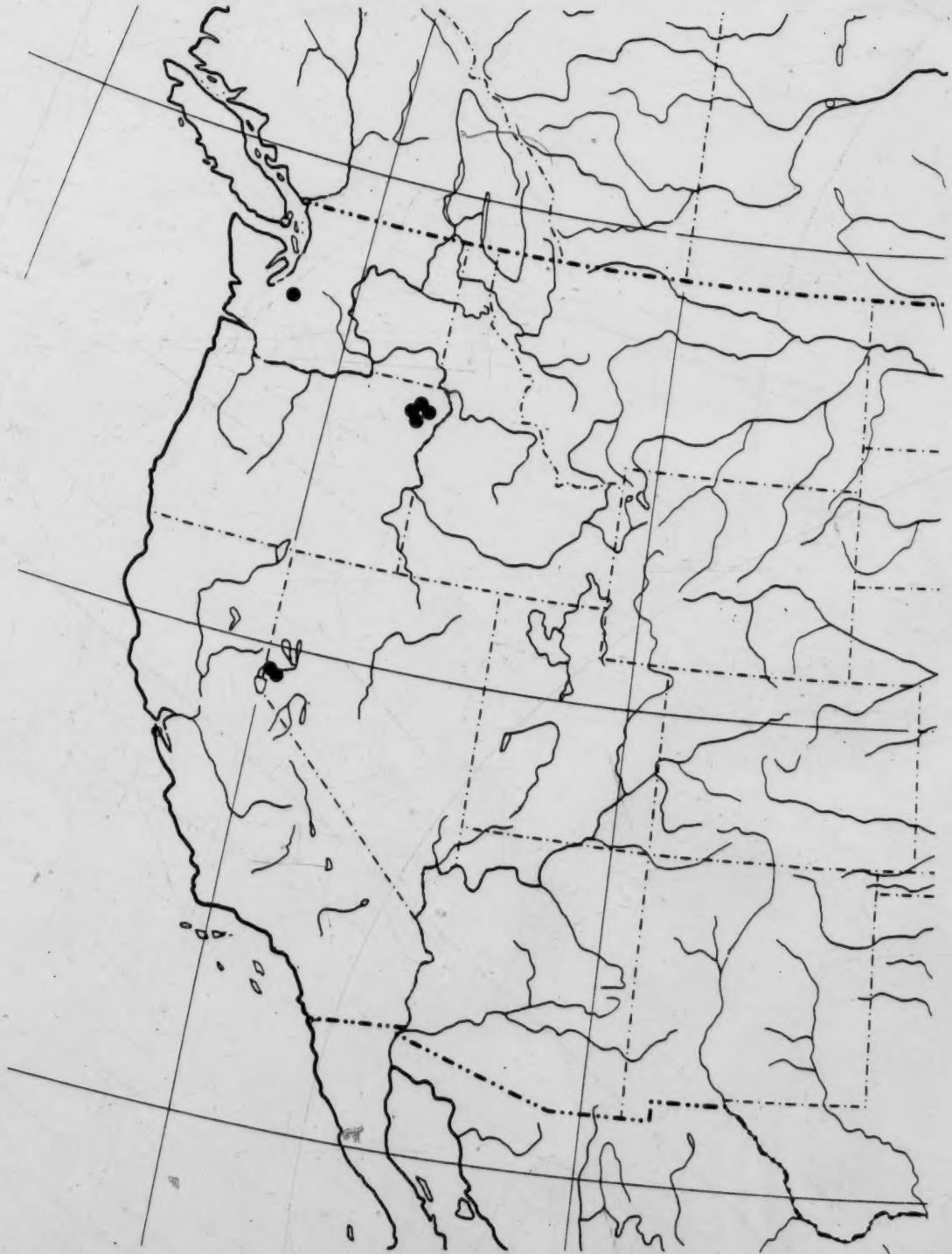
Wallowa County: Ice Lake, Wallowa mountains.

Elevation: 2000m.

Collected by: J. Bain #199.

HOLOTYPE 25/07/81

Figure 22. Distribution of *Senecio wallowensis* Bain



2308, UC! US!). Other than this latter collection *S. porteri* has only been found in Colorado. The two species are structurally similar in having widely ovate leaves with sub-cordate bases (Barkley, 1962, describes the leaves of *S. porteri* as reniform) and both have a disjunct, albeit different, distribution pattern. Weber (1965) cites the distribution pattern of *S. porteri* as evidence that it is an Arcto-Tertiary relict. Further study of these two taxa may uncover a link between the alpine aureoid senecios (*cf.* Packer, 1972) and the *S. streptanthifolius* complex. The close relationship between *S. wallowensis* and *S. laetiflorus* has been previously discussed.

Senecio kluanei *sp. nov.*

Type: Haines Junction, Yukon Territory. *Bain 152* ALTA (holotype). Figure 23.

Herbaceous perennial, 2-3 dm tall, glabrous or occasionally very lightly tomentose at the base of the involucres; stems 1-2, arising from a fibrous root stock; basal leaves turgid and leathery in texture, petiolate, the petioles 2.5-4.0 cm long, blades obovate to widely oblanceolate, cuneate or narrowly cuneate at the base, margins serrate near the base and serrate or dentate near the apex, 1.5-3.5 cm long, 0.8-1.4 cm wide; cauline leaves few, entire to subentire and bract-like; inflorescence a congested, sub-umbelliform cyme of 5-13 heads; involucral bracts 15-19, 5.0-6.0 mm long; achenes glabrous; n = 46.

DISTRIBUTION: Open disturbed sites in southern Yukon and northern British Columbia. Figure 24.

DISCUSSION: *Senecio kluanei* is undoubtedly an alloploid species but its origins are somewhat unclear. It has been collected only on disturbed roadside sites and as such it appears to be a successional species. However this habitat is also occupied by *S. streptanthifolius* var. *borealis* so it is not here presented

Figure 23. Holotype of *Senecio kluanei* Bain

FLORA OF YUKON TERRITORY

Senecio kluanei Bain n. sp.

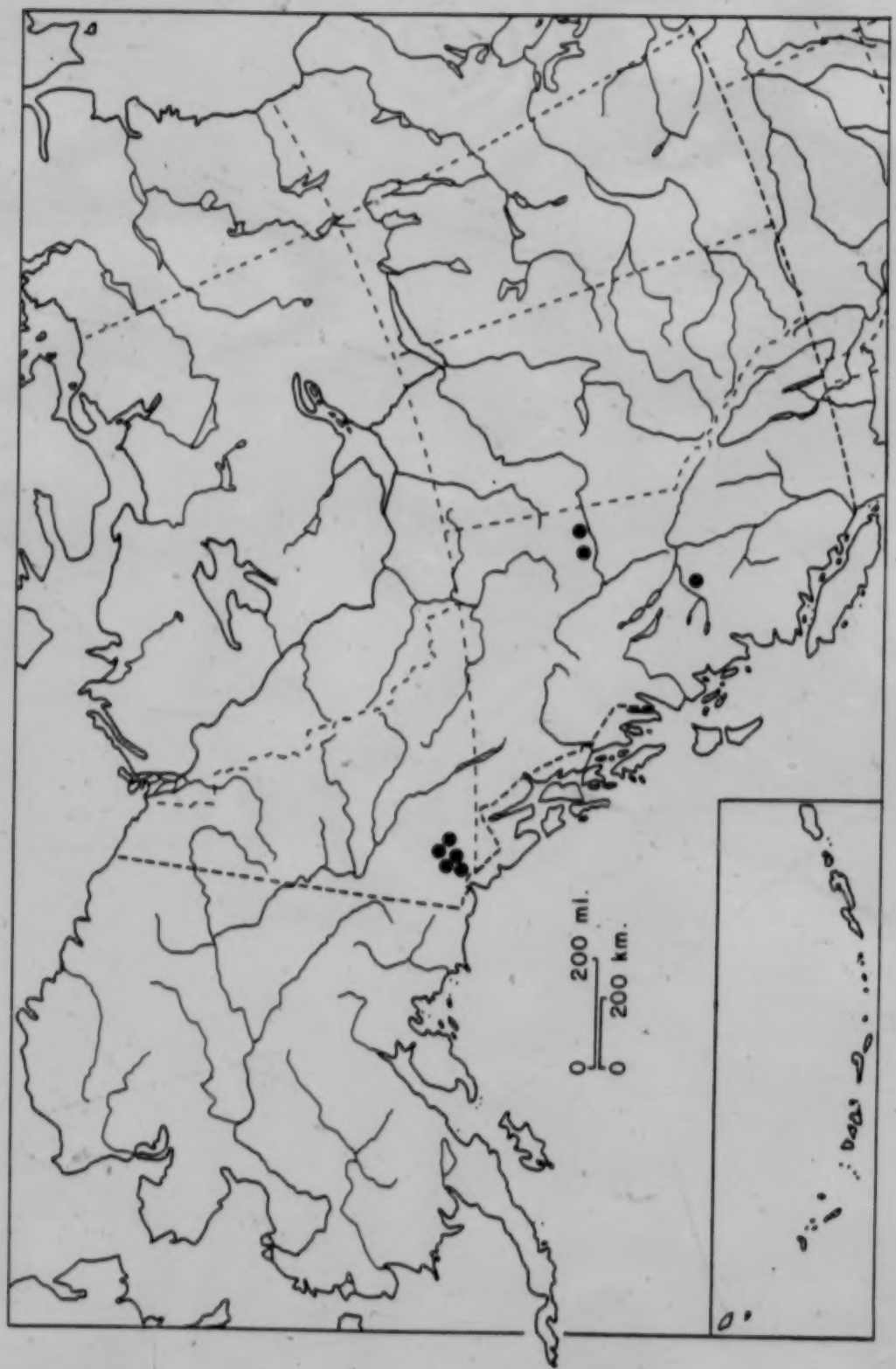
1 km. east of Haines Junction on Hwy 91
(Alaska Highway)

Collected by: J. Bain #152

3/07/81

HOLOTYPE

Figure 24. Distribution of *Senecio kluanei* Bain


0 200 mi.
0 200 km.

as a distinguishing feature for the species.

There are undeniable structural affinities with *S. pauperculus* including dentate-serrate lower leaf margins, disc floret length, disc floret number and phyllary number; however the flavonoid profile of *S. kluanei* does not indicate any relationship to *S. pauperculus*.

Senecio kluanei may also be related to *S. ogotorukensis* Packer, a diploid aureoid senecio inhabiting the same area. The leaf margins of *S. ogotorukensis* are, according to Packer (1972), very variable, ranging from entire to deeply serrate to regularly or pinnately lobed. The margins of *S. kluanei* fall somewhere in between these and the weakly crenate-dentate margins of *S. pauperculus*. Examination of one of the populations of *S. kluanei* revealed a large number of monocephalous individuals which may possibly be construed as evidence of a relationship with *S. ogotorukensis* which also has few heads but once again, the evidence is not supported by flavonoid profiles. Although no compounds were identified for *S. ogotorukensis*, examination of two-dimensional chromatograms revealed a depauperate profile of between three and four compounds, whereas *S. kluanei* contains ten.

Senecio kluanei appears from herbarium specimens to extend into northern British Columbia (McCabe 704, Rice 55, Raup and Abbe 4163). One southern population (Hitchcock and Martin 7409) collected from south of Savona, British Columbia bears some resemblance, however, the inflorescence is more corymbose and guard cell lengths indicate the specimen is diploid. (see Table 11)

VII. Discussion and Conclusions

The present treatment represents a radical departure from that of Barkley (1978). Seven taxa (including five species) are now recognized where Barkley had recognized one. On the other hand, six of the seven taxa had been previously recognized at least in some approximate form and over all, the proposed classification closely approximates that of Greenman (1916).

Numerical analyses, using equal character weighting, have clearly shown that specimens from the *S. streptanthifolius* complex do cluster into discrete groups, although the groups are often closely related. Furthermore, a number of characters in addition to leaf characters were identified as useful in separating the presently recognized taxa. However, in no case was a single structural character found to be diagnostic for a taxon.

Chromosome studies have shown that chromosome number is relatively constant within the complex and therefore generally not a source of phenotypic variation. No evidence for aneuploidy was found and polyploidy was relatively uncommon. When present, it was generally associated with suspected hybridization or introgression.

Flavonoid profiles were found to be relatively simple with respect to aglycone diversity however a high degree of variation was found in the number and types of sugars attached to the flavonoid molecule. Taxa were sometimes separable based on their possession of a specific class of flavonoid compound; *i.e.* isorhamnetin 3-O glycosides, rather than on the presence or absence of a single compound.

All of these variation patterns support the idea that species within the *S. streptanthifolius* complex are not well defined and that genetic differences are not great. The predominant pattern in structural characters is one of extensive range overlap and in flavonoid characters where character states are necessarily mutually exclusive most differences occur in glycosylation patterns. Brederode and Nigtevecht (1972) showed that glycosylation of isovitexin in *Melandrium album* was controlled by three genes, each one controlling a different sugar substitution. The flavonoid differences in the *S. streptanthifolius* complex are

therefore not considered to be indicative of gross genetic differences between species, but the relative intra-specific constancy of the characters indicates that the differences are real. Speciation via ecological isolation has already been mentioned as a likely mode of speciation acting within the *S. streptanthifolius* complex and certainly this mode could easily produce the pattern of gradual differentiation shown in this study. Superimposed upon this pattern of gradual differentiation is another pattern, more obvious in the aureoid complex as a whole, whereby more clearly defined species or clusters of species are apparent. This suggests that speciation within the aureoid complex is occurring in stages. In the Phytogeography section it was postulated that some differentiation of taxa had occurred during the Pliocene while other taxa originated more recently during the Pleistocene. Introgression was also postulated as underlying some of the speciation which had occurred within the aureoid complex. This differentiation, followed by reunion of sorts through introgression, would result in the reticulate pattern of relationships apparent among some of the species today.

Species of the *S. streptanthifolius* complex exhibit a number of characters which are responsible to a large degree for the complex variation pattern shown. They are:

1) high fecundity
2) dispersability
3) self sterility
4) non specificity with respect to pollinators

All of these characters contribute to the maintenance of a diverse gene pool within populations. As well as resulting in structural variability this would also allow populations to adapt easily and occupy different environments. Limitations to genetic exchange are seen as coming mainly from polyploidy as well as external factors such as spatial or ecological isolation, the latter two being less effective than the first. Longterm isolation of small populations, such as has possibly occurred for *S. porteri* would likely result in decreased variability through inbreeding. Schofield (1969) pointed out that endemic species of polymorphic genera like *Senecio* are often unusually distinct. Genetic homogeneity

was also described by Kowal (1975) as a trait of the self-compatible species *S. indecorus*. In this latter species, isolation results from polyploidization (to the octaploid level). Kowal postulated that the self-fertility character arose after populations were isolated by polyploidization since it would be selected for in smaller populations where inbreeding depression is counteracted by genome replication. Finally, *S. debilis* may also be an example of a species which has developed genetic homogeneity, this time through ecological isolation. *S. debilis* was described by Barkley (1962) as "one of the more distinctive species in the *Aurei*". Like *S. laetiflorus*, *S. debilis* is restricted to alkaline meadow habitats but occurs further east in Idaho and Wyoming. It seems likely that this habitat specificity has acted as a form of ecological isolation which, like the previous examples, has resulted in a level of phenotypic and therefore presumably genetic uniformity unusual among aureoid species.

In the *S. streptanthifolius* complex isolation has probably played a role in speciation on numerous occasions; the most clear-cut being the polyploidization of *S. kluanei* and its subsequent isolation. *Senecio wallowensis* has probably been subjected to the same geographical isolation as has *S. porteri* and the habitat preference of *S. laetiflorus* may be acting as a form of ecological isolation just as it apparently does in *S. debilis*. No obvious isolating factors are present for *S. oodes*, however the fact that it remains distinct, structurally and phytochemically even though it occurs sympatrically with a number of aureoid species, suggests that some means of isolation exists. *Senecio streptanthifolius* is the species which is clearly not genetically isolated from a number of other aureoid species. Introgression with *S. neomexicanus*, *S. multilobatus*, and *S. tridenticulatus* is considered here to have in part resulted from and in turn contributed to the variability of the species. In the case of *S. streptanthifolius* var. *rubricaulis* polyploidization has undoubtedly effected the genetic isolation of some populations; however unlike in the case of *S. kluanei*, diploid populations in the same vicinity exhibit a similar structural and phytochemical phenotype. So, although it is acknowledged as likely that tetraploid populations of var. *rubricaulis* will, in ensuing generations become increasingly distinct, they are not now

different enough to be considered a new species. *Senecio streptanthifolius* var. *borealis* is considered to have arisen as a result of the ability of *S. streptanthifolius* to move into and adapt to new territories. Although populations of var. *borealis* become more and more isolated from var. *streptanthifolius* as one moves north, no geographical isolation exists between the taxa farther south and in this region they intergrade with with one another. Structural characters allow the separation of the two taxa but their close relationship is best represented by treating them as varieties of the same species.

One of the reasons given in the introduction for studying the *S. streptanthifolius* complex was to provide a foundation for work in the rest of the aureoid complex. The present study does provide basic information of relevence to the rest of the complex.

From a utilitarian standpoint, sixteen structural characters have been identified which show significant differences between the taxa studied. Some of the characters have been used only sporadically in the past and undoubtedly they will prove useful in separating other taxa in the complex. Of these, disc floret length and number are perhaps the easiest to measure. The data base used in the numerical analysis can be easily expanded to include and compare other species.

Chromosome numbers are now more completely known. Anomalies like aneuploidy and hybridization across ploidy levels are apparently rare. Sources for variation must therefore be found elsewhere. Electrophoretic studies of isozyme variability may provide more insight into how much genetic variability exists within a population.

A foundation has also been laid for further flavonoid studies within the complex. Flavonoid patterns are so far all very similar, revolving around a few simple flavonol and flavone molecules, to which a wide array of sugars have been attached. As well as continuing to provide a method of comparing species, the overall pattern of these profiles may remain constant enough to be useful in defining the aureoid complex as a whole, or at least large parts of it.

On a more theoretical level, the inferences derived from both the cladistic and phytogeographic portions of this study have implications for the rest of the complex which clearly must be investigated. Incorporation of data from related species will allow more accurate assessment of phylogenetic trends and the testing of those currently proposed. The fact that the current study postulated hybridization involving parents which could not be depicted on the cladogram because they were outside the complex studied, underlines the necessity for incorporating and comparing more studies in order to achieve a broader base.

In summary, the current study proposes that *S. streptanthifolius* as recognized by Barkley (1962, 1978) be split into seven taxa - five species and two varieties. The new arrangement is thought to reflect more accurately the evolutionary history of the group while at the same time it provides a clear phenotypic definition for each of the taxa proposed. Hybridization and genetic isolation resulting from polyploidization, geographical isolation, or ecological isolation are thought to have played a major role in speciation, producing genetically homogeneous species of somewhat localized distribution, as well as genetically variable and geographically wide-ranging species. *S. wallowensis, S. kluanei, S. laetiflorus* and possibly *S. oodes* fall into the former category. *Senecio streptanthifolius* although it is defined more narrowly in this study than in the past still qualifies as one of the latter types. *S. pauperculus, S. multilobatus* and *S. neomexicanus* are also of this latter type.

Evolution in the *S. streptanthifolius* complex is apparently continuing via the same means as in the past. Populations of *S. streptanthifolius* var. *rubricaulis* have become genetically isolated via polyploidization and it is postulated that in time these populations will become established and sufficiently differentiated to be considered a distinct species.

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Appendix 1. - Populations used for flavonoid analysis

TAXON	n	LOCATION	*COLL. NO.
S. canus	69	B.C.: between Cranbrook and Ft. Steele	050
	46	CA.: 12 km. N. of Weed on Hwy. 97	041
	23	OR.: along Hwy 199, ca 4.8 mi. N. of Obrien	039
	46	OR.: 64 km. E. of Klamath Falls	038
	23	OR.: 45 km W. of John Day	048
	23	OR.: ca 16 km. N. of Burns on #395	047
S. kluanei	46	YUKON: 1 km. E. of Haines Jctn on Hwy #1 (Alaska Hwy)	152B
	46	YUKON: km. 1538 - Alaska Hwy, W. of Whitehorse	153

	46	YUKON: Lake Labarge	154
S. laetiflorus[1]	23	CA.: 3.2 km. S. of Gazelle	040
S. multilobatus	23	NV.: along Hwy 93, ca. 90 km. S. of Ely	027
	46	NM.: on Burro Mtn. south of Silver City	007
	46	UT.: along road to Panaca, Nevada	026
	23	CO.: Plumtaw Rd., NW of Pagosa Springs	094
S. neomexicanus var. *metcalfei*	46	NM.: 20 km. N. of Silver City	005
	46	NM.: Hwy#90 - 16 km. W. of Kingston	003
S. neomexicanus var. *mutabilis*	23	UT.: 2 km W. of Monticello	022
	23	CO.: W. of Silverton on Hwy#550	093
S. neomexicanus var. *neomexicanus*	23	AZ.: 12.8 km. S. of Showlow	010

	23	NM.: along Hwy#90, 0.4 km W. of Emory Pass	001
S. oodes	23	CO.: 7 km E. of Red Cliff	105
	23	CO.: E. side of Wolf Creek Pass	096
	23	CO.: E. side of Wolf Creek Pass	096A
	23	WY.: 2.5 km W. of Bear River	080
S. pauperculus	46	ALTA.: 30 km N. of Whitecourt along Hwy#43	062
	46	ALTA.: Kananaskis Lake at south end of Lower Lake	79022
	46	B.C.: 20 km S. of Savona	056
	46	B.C.: ca. 18 km S. of Savona	059
	23	B.C.: km 775 - Hwy 97 (Alaska Hwy)	165
	23	B.C.: km 696-Alaska Hwy.	168

	ca. 46	NWT: 10 km. S. of Hay River	063
	46	NWT: 20 km S. of Enterprise	064
	46	NWT: km. 116 - Hwy#1, 32 km. W. of Enterprise	070
S. pseudaureus var. *flavulus*	23	ID.: E. of Leslie, SE of Mackay	076
S. streptanthifolius var. *borealis*	23	B.C.: 20 km. S. of Savona	054
	23	B.C.: roadside between 70 Mile House and Green Lake Park	061
	23	B.C.: ca. 40 km. W. of Dease Lake on road to Telegraph Creek	126
	23	B.C.: ca. 12.8 km. N. of Dease Lake along Hwy #37(Cassian Hwy.)	131
	23	B.C.: ca. 64 km. N. of Atlin	137

	23	YUKON: between Tagish & Jake's Corners	138
	23	YUKON: 3.2 km. N. of Carcross	139
S. streptanthifolius var. *rubricaulis*	46	UT.: vicinity of Naomi Pk.	078
	23	UT.: ca. 2 km E. of Elizabeth Pass	083
	23	UT.: 12 km. W. of Elizabeth Pass	084
	23	UT.: S. of Lilly Lake & Lost Lake	085
	46	WY.: 14.5 km. N. of Hwy 187-189, N. of Bondurant	106
	46	WY.: 16 km. W. of Hwy. 187-189 on Hwy#22 toward Teton Pass	107
	23	WY.: ca. 10km. N. of Moran	108
S. streptanthifolius var. *streptanthifolius*	23	CA.: Sonora Pass - Sweetwater Mtns.	206

	23	MT.: 3.3 km S. of Cascade Co. line at King's Hill Pass	109
	23	WA.: Wanatchee Mtns.- Iron Creek Trail, ca. 16 km. NNE of Cle Elum	205
S. streptanthifolius X pauperculus	46	ID.: ca. 11.2 km. SE. of Baker	075
S. wallowensis[1]	23	OR.: Ice Lake, Wallowa Mtns.	199

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* all collections were made by the author

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[1]data were augmented by profiles run from single leaf extracts of herbarium specimens

Appendix 2 - Data matrix for numerical analysis

otu 001 01.0 20.0 00.0 00.0 7.0 4.2 03.0 01.0 00.0 17.0 00.0
01.0 00.0 00.0 07.0 04.0 06.0 999 06.0 02.0 0.0 6.0 03.0 06.0 11.0 45.0 10.0
06.0 14.0 01.10 04.09 036.0 1.012 0.921 0.866 .4087 02.12 1.02 2.30 999
999 999 999 999 999 999 999 999 999 999 999
otu 002 00.0 19.5 00.0 00.0 7.0 05.0 05.0 00.0 00.0 27.0 01.0
03.0 00.0 00.0 06.0 05.0 08.0 11.0 05.0 02.0 0.0 05.5 2.5 6.0 10.0 34.0 999.
05.0 17.0 01.20 06.36 15.97 .9784 0.883 0.807 .3085 02.62 1.07 2.97 999
999 999 999 999 999 999 999 999 999 999 999
otu 003 01.0 25.0 00.0 00.0 3.0 02.0 05.0 00.0 00.0 13.0 00.0
01.0 00.0 00.0 06.0 02.0 04.0 11.0 04.0 1.3 0.0 6.0 2.5 5.0 7.5 39.0 999
05.0 15.0 01.45 04.94 55.41 1.135 01.13 01.22 .4921 02.47 1.06 2.19 999
999 999 999 999 999 999 999 999 999 999 999
otu 004 00.0 22.5 00.0 00.0 03.0 03.0 02.0 01.0 00.0 20.0 01.0
02.0 00.0 00.0 05.0 02.0 04.0 07.0 05.0 02.0 00.0 5.0 1.8 5.5 10.7 25.0 999
4.8 10.0 01.45 05.44 091.0 01.07 01.56 0.848 .4401 01.93 1.02 1.24 01
01 00 00 00 01 00 01 00 01 00 00
otu 005 01.0 24.0 00.0 00.0 5.0 04.0 04.0 01.0 00.0 05.0 00.0
01.0 01.0 01.0 06.0 02.0 05.0 11.0 03.0 0.5 00 4.0 1.8 999 999 42.0 07.0
05.0 14.0 02.10 11.27 017.0 00.97 01.66 01.59 .3344 04.74 1.08 2.86 01
01 00 00 00 01 00 01 00 01 00 00
otu 006 00.0 28.0 00.0 00.0 5.0 4.7 09.0 01.0 00.0 17.0 00.0
01.0 00.0 00.0 05.0 02.0 04.0 09.0 05.0 2.0 00 6.0 2.3 5.3 10.5 54.0 10.0
05.0 19.0 01.55 08.03 019.0 01.07 01.00 01.42 .4007 03.54 1.03 3.54 999
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otu 007 01.0 26.3 00.0 10.0 10.0 3.2 03.0 01.0 01 0 20.0 02.0
05.0 00.0 00.0 06.0 2.5 04.0 06.0 5.5 1.5 1.0 6.0 2.2 999. 08.0 26.0 999.
06.0 12.0 01.66 13.04 070.0 .8398 01.63 01.37 .4456 03.07 1.76 1.88 01
01 01 00 00 00 00 00 00 01 00 00
otu 008 01.0 23.0 02.0 00.0 7.0 3.2 04.0 01.0 00.0 15.0 00.0
01.0 01.0 01.0 07.0 03.0 06.0 11.0 06.0 01.0 01.0 6.2 2.7 999. 999. 45.0 08.0
06.0 17.0 01.47 16.07 048.0 00.58 01.83 01.57 .5728 02.74 2.13 1.50 00
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otu 009 01.0 24.3 01.0 10.0 10.0 3.0 05.0 01.0 01.0 23.0 04.0
06.0 00.0 00.0 06.0 02.0 4.5 07.0 05.0 1.6 01.0 07.0 2.7 999. 07.0 23.0 01.0
06.0 12.0 02.56 11.19 046.0 01.12 02.16 01.87 .4100 04.57 1.05 2.12 999
999 999 999 999 999 999 999 999 999 999 999
otu 010 00.0 26.2 01.0 10.0 10.0 4.9 08.0 01.0 01.0 24.0 07.0
02.0 00.0 00.0 06.0 03.0 05.0 06.0 05.0 1.2 00.0 5.8 2.3 999. 999. 38.0 999.
06.0 15.0 03.20 14.18 130.0 .5997 02.47 02.51 .5678 04.41 1.26 1.79 00
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otu 011 00.0 23.0 01.0 10.0 10.0 2.6 09.0 01.0 01.0 17.0 06.0
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05.0 16.0 01.93 036.0 140.0 .4414 01.98 04.76 .6342 07.51 2.23 3.79 01
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otu 012 01.0 62.0 00.0 10.0 7.0 8.2 05.0 00.0 01.0 09.0 03.0

02.0 01.0 01.0 06.0 05.0 08.0 11.0 06.0 1.6 00.0 5.4 2.5 6.4 11.7 96.0 11.0
06.0 21.0 06.39 18.05 999.0 .7668 3.34 5.69 .5293 10.75 1.64 3.22 00
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otu 013 00.0 19.0 03.0 0.0 0.0 3.8 05.0 01.0 0.0 05.0 05.0
01.0 02.0 02.0 07.0 02.0 4.8 06.0 04.0 1.4 00.0 6.2 2.3 5.0 999. 23.0 999
06.0 15.0 2.80 2.27 14.0 .9897 1.03 1.06 .2972 3.57 1.01 3.47 01
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otu 014 00.0 17.2 03.0 0.0 0.0 1.8 05.0 00.0 00.0 06.0 03.0
03.0 02.0 02.0 10.0 05.0 09.0 14.0 6.5 3.0 00.0 8.5 2.7 8.5 15.0 47.0 999.
09.0 17.0 2.74 2.38 35.0 1.076 1.07 1.65 .4798 3.44 1.02 3.21 00
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otu 015 01.0 32.0 00.0 4.0 4.0 5.0 08.0 01.0 00.0 05.0 00.0
01.0 00.0 00.0 07.0 02.0 4.5 08.0 05.0 999. 00.0 5.5 2.2 999. 999. 30.0 08.0
06.0 10.0 02.30 12.03 018.0 1.010 02.02 01.53 .3394 04.51 1.18 2.23 01
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otu 016 01.0 33.0 00.0 0.0 3.0 03.0 07.0 01.0 00.0 12.0 00.0
01.0 00.0 00.0 05.0 03.0 5.5 08.0 6.5 1.5 00.0 5.2 2.0 5.5 9.6 34.0 999.
4.5 14.0 01.23 05.21 043.0 1.087 0.986 0.945 .4408 02.14 1.05 2.17 01
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otu 017 01.0 37.0 02.0 7.0 7.0 3.2 04.0 01.0 01.0 07.0 01.0
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08.0 20.0 01.75 09.34 018.0 0.998 1.47 01.61 .4561 03.57 1.18 2.43 00
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otu 018 01.0 38.0 00.0 0.0 7.0 3.6 14.0 01.0 00.0 06.0 00.0
01.0 01.0 01.0 07.0 04.0 7.0 14.0 05.0 1.3 00.0 6.0 2.2 5.0 15.0 60.0 09.0
06.0 16.0 0.990 04.69 012.0 1.010 0.77 0.990 .4575 01.99 1.06 2.58 999
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otu 019 02.0 67.0 01.0 5.0 6.0 07.0 07.0 01.0 01.0 06.0 00.0
01.0 01.0 01.0 13.0 05.0 08.0 12.0 4.2 0.9 00.0 7.8 2.4 999. 11.0 81.0 07.0
13.0 12.0 02.41 11.64 049.0 01.03 2.29 02.04 .5367 03.80 1.21 1.66 999
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otu 020 01.0 55.0 00.0 5.0 5.0 3.3 05.0 00.0 01.0 15.0 00.0
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12.0 16.0 02.61 18.92 060.0 .6488 3.54 01.95 .3931 04.97 1.48 1.40 00
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otu 021 01.0 38.0 00.0 0.0 4.0 2.1 04.0 01.0 01.0 15.0 03.0
01.0 00.0 00.0 05.0 02.0 05.0 08.0 3.7 2.2 00.0 5.3 2.5 5.0 11.0 39.0 999.
05.0 13.0 01.12 04.89 041.0 01.00 1.14 0.420 .2285 01.84 1.05 1.61 01
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otu 022 0.5 28.0 00.0 0.0 4.0 2.3 04.0 01.0 00.0 06.0 00.0
01.0 00.0 00.0 06.0 04.0 06.0 07.0 4.5 1.8 00.0 5.0 2.1 5.5 09.0 37.0 999.
05.0 11.0 01.26 07.43 020.0 001.2 0.83 0.703 0.276 02.55 1.07 3.07 01
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01.0 00.0 00.0 06.0 03.0 07.0 11.0 5.8 1.8 00.0 6.5 2.3 6.0 09.0 31.0 8.0
05.0 13.0 01.30 07.08 007.0 001.1 0.874 0.886 0.279 03.17 1.04 3.63 01

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01.0 01.0 01.0 5.5 02.0 4.5 09.0 5.0 2.0 00.0 6.5 2.8 6.2 12.0 29.0 08.0
05.0 13.0 0.960 05.06 016.0 01.04 0.691 0.603 .2843 02.12 1.08 3.07 01
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otu 025 01.0 30.5 00.0 6.0 6.0 2.5 05.0 00.0 00.0 13.0 00.0
01.0 00.0 00.0 07.0 03.0 05.0 09.0 5.5 1.8. 00.0 7.0 3.0 7.2 14.0 48.0 11.0
06.0 21.0 01.51 07.74 031.0 01.08 1.060 01.72 .5086 03.38 1.07 3.19 01
01 01 00 00 01 00 01 00 01 00 00
otu 026 1.5 46.0 00.0 9.0 8.0 7.7 7.0 01.0 01.0 11.0 00.0
01.0 00.0 00.0 06.0 03.0 05.0 07.0 5.5 1.7 00.0 6.5 2.8 6.0 14.0 40.0 09.0
5.5 13.0 02.76 19.55 054.0 00.92 2.91 02.97 .6621 04.49 1.67 1.54 00
01 01 01 00 00 00 00 00 01 00 00
otu 027 1.5 48.5 00.0 5.0 6.0 05.0 07.0 01.0 00.0 08.0 00.0
01.0 00.0 00.0 05.0 03.0 06.0 11.0 5.5 2.1 00.0 7.5 3.2 7.3 12.0 51.0 09.0
6.1 21.0 02.34 11.19 020.0 01.05 1.99 01.89 .4612 04.09 1.19 2.06 00
01 01 01 00 00 00 00 00 01 00 00
otu 028 1.5 43.0 01.0 7.0 7.0 05.0 06.0 01.0 00.0 10.0 00.0
01.0 00.0 03.0 05.0 03.0 06.0 09.0 05.0 1.4 00.0 6.5 2.4 999. 9.8 63.0 999.
06.0 21.0 02.04 8.32 35.0 1.20 1.42 1.25 .3745 3.33 1.05 2.35 01
01 01 00 00 00 00 00 00 01 00 00
otu 029 03.0 26.3 00.0 9.0 9.0 1.8 04.0 01.0 01.0 13.0 01.0
02.0 00.0 00.0 04.0 1.5 04.0 08.0 06.0 1.2 00.0 6.2 2.8 999. 08.0 29.0 999.
3.8 18.0 01.62 17.54 131.0 00.69 1.41 01.57 .3909 04.01 1.89 2.84 00
01 01 01 00 00 00 00 00 01 00 00
otu 030 00.0 32.0 00.0 9.0 4.0 2.9 03.0 01.0 01.0 11.0 00.0
01.0 00.0 00.0 05.0 02.0 05.0 11.0 5.5 2.5 00.0 6.0 3.0 6.2 11.0 31.0 999.
06.0 15.0 01.42 13.43 32.0 .6394 1.22 1.70 .4686 3.62 1.67 2.97 00
01 01 01 00 00 00 00 00 01 00 00
otu 031 03.0 37.0 01.0 9.0 8.0 6.2 06.0 01.0 01.0 31.0 01.0
06.0 00.0 00.0 06.0 03.0 06.0 07.0 05.0 2.5 01.0 6.5 2.8 6.0 11.0 26.0 06.0
05.0 14.0 01.61 10.83 071.0 00.79 1.57 01.11 .3934 02.83 1.56 1.80 01
01 01 00 00 00 00 00 00 01 00 00
otu 032 00.0 22.5 00.0 9.0 8.0 13.0 07.0 01.0 01.0 22.0 02.0
01.0 00.0 00.0 05.0 02.0 04.0 07.0 04.0 1.9 01.0 6.0 3.0 6.0 09.0 26.0 08.0
06.0 12.0 01.30 10.09 45.0 .8192 1.18 0.717 .3448 2.08 1.41 1.76 01
01 01 00 00 00 00 00 00 01 00 00
otu 033 0.5 31.5 02.0 7.0 4.0 2.5 02.0 01.0 00.0 10.0 00.0
01.0 01.0 03.0 04.0 02.0 04.0 08.0 4.2 1.0 00.0 6.3 2.0 7.2 10.0 35.0 999.
05.0 12.0 01.93 8.13 24.0 1.15 1.69 1.42 .4240 3.35 1.05 1.98 01
01 00 00 00 01 00 00 00 00 00 00
otu 034 01.0 14.5 02.0 0.0 7.0 2.2 01.0 01.0 00.0 05.0 00.0
01.0 02.0 03.0 05.0 02.0 06.0 08.0 4.0 1.7 01.0 5.8 2.8 5.5 07.0 39.0 06.0
04.0 17.0 1.22 19.80 17.0 0.98 0.966 1.09 .4558 2.40 1.04 2.48 01
01 00 00 00 01 00 00 00 01 00 00
otu 035 0.5 40.0 02.0 4.0 4.0 07.0 07.0 01.0 01.0 16.0 06.0

04.0 02.0 03.0 05.0 02.0 4.5 6.0 3.5 2.0 00.0 6.0 2.2 5.5 06.0 38.0 999.
04.0 14.0 2.28 5.44 66.0 1.22 2.39 1.29 .4264 3.03 1.13 1.27 01
01 01 00 00 00 00 00 00 01 00 00
otu 036 01.0 20.8 03.0 9.0 9.0 1.2 08.0 01.0 01.0 999. 05.0
01.0 02.0 03.0 06.0 2.5 04.0 06.0 6.0 1.2 00.0 6.0 3.0 5.8 09.0 39.0 06.0
04.0 16.0 1.13 11.53 999.0 0.750 .920 1.88 .6428 2.92 1.56 3.17 00
01 00 00 00 00 00 00 00 00 00 00
otu 037 01.0 15.0 03.0 1.0 6.0 2.2 05.0 01.0 00.0 08.0 00.0
01.0 01.0 03.0 05.0 02.0 5.0 8.0 5.0 2.0 00.0 6.0 2.8 5.5 08.0 30.0 08.0
05.0 13.0 0.850 4.07 5.0 .920 .697 .791 .4553 1.74 1.03 2.50 01
01 01 00 00 00 00 00 00 01 00 00
otu 038 01.0 39.0 02.0 5.0 7.0 09.0 04.0 01.0 01.0 11.0 00.0
01.0 02.0 03.0 06.0 03.0 05.0 7.5 4.5 2.2 00.0 6.0 2.2 6.0 10.0 49.0 08.0
05.0 17.0 2.65 13.98 50.0 1.16 2.59 2.14 .5476 3.91 1.43 1.51 01
01 01 00 00 00 00 00 00 01 00 00
otu 039 01.0 46.0 00.0 9.0 4.0 06.0 06.0 00.0 01.0 07.0 01.0
01.0 00.0 00.0 06.0 03.0 06.0 10.0 4.0 2.3 00.0 8.0 3.2 8.2 12.0 39.0 08.0
06.0 16.0 2.35 12.12 142.0 1.07 2.29 1.53 .4836 3.17 1.36 1.38 01
01 01 00 00 01 00 00 00 00 00 00
otu 040 00.0 44.0 00.0 8.0 5.0 5.6 04.0 01.0 01.0 13.0 02.0
02.0 00.0 00.0 06.0 02.0 04.0 09.0 06.0 2.0 00.0 6.8 3.0 7.0 11.2 25.0 06.0
5.5 13.0 2.08 11.34 15.0 .954 2.05 1.67 .4562 3.66 1.29 1.79 01
01 00 00 00 01 00 00 00 00 00 00
otu 041 00.0 32.0 00.0 4.0 7.0 2.5 05.0 01.0 01.0 19.0 00.0
01.0 00.0 00.0 06.0 2.8 7.0 9.0 4.0 1.7 00.0 6.0 2.5 6.4 8.1 43.0 10.0
5.0 21.0 1.53 9.09 85.0 .884 1.40 1.03 .3491 3.04 1.30 2.17 01
01 01 00 00 01 00 00 00 00 00 00
otu 042 01.0 32.0 00.0 0.0 4.0 2.5 05.0 01.0 00.0 21.0 01.0
06.0 00.0 00.0 4.7 02.0 4.0 6.5 4.5 2.0 00.0 6.0 2.5 6.0 8.2 42.0 06.0
05.0 15.0 1.88 8.44 28.0 1.01 1.74 1.09 .3180 3.42 1.04 1.97 01
01 01 00 00 01 00 00 00 00 00 00
otu 043 01.0 23.0 00.0 0.0 7.0 4.5 02.0 01.0 00.0 15.0 00.0
0410 00.0 00.0 4.0 2.4 5.0 9.0 5.0 1.4 00.0 6.0 2.8 6.8 8.5 40.0 999.
04.0 13.0 1.45 7.43 19.0 0.972 1.11 0.74 .2415 3.06 1.06 2.76 01
01 00 00 00 01 00 01 00 01 00 00
otu 044 00.0 22.5 00.0 1.0 7.0 03.0 03.0 01.0 00.0 09.0 00.0
01.0 00.0 00.0 4.2 2.0 3.0 6.0 5.0 1.3 00.0 5.0 2.3 6.0 7.8 51.0 999.
4.3 14.0 1.10 4.47 58.0 1.11 1.11 0.680 .4248 1.60 1.10 1.44 999
999 999 999 999 999 999 999 999 999 999 999
otu 045 01.0 26.0 00.0 0.0 7.0 03.0 03.0 00.0 00.0 11.0 02.0
01.0 00.0 00.0 4.2 3.0 4.2 8.0 3.8 1.0 00.0 5.5 2.3 6.1 9.8 42.0 08.0
4.1 19.0 1.01 4.91 27.0 1.06 0.740 0.674 .3226 2.09 1.05 2.82 01
01 00 00 00 01 00 01 00 01 00 00
otu 046 04.0 23.0 00.0 2.0 3.0 04.0 04.0 01.0 01.0 27.0 01.0
02.0 00.0 00.0 05.0 02.0 3.5 7.0 5.7 1.5 00.0 5.5 2.5 5.7 8.0 27.0 08.0
05.0 12.0 1.48 5.89 50.0 1.13 1.42 0.840 .3580 2.35 1.04 1.65 01

01 00 00 00 01 00 01 01 01 00 00
otu 047 01.0 47.0 00.0 0.0 7.0 2.5 07.0 00.0 00.0 35.0 03.0
01.0 00.0 00.0 5.0 2.8 5.3 7.5 4.2 1.2 00.0 6.5 2.7 6.0 08.0 43.0 999.
05.0 17.0 1.62 9.15 9.0 .998 1.12 1.03 .2569 4.01 1.02 3.58 01
01 00 00 00 01 00 01 01 01 00 00
otu 048 01.0 30.5 00.0 2.0 7.0 5.5 05.0 01.0 00.0 19.0 00.0
01.0 00.0 00.0 4.0 2.0 4.0 8.0 4.5 1.2 00.0 5.3 2.3 5.5 8.5 31.0 07.0
04.0 13.0 1.52 6.35 54.0 1.09 1.35 1.06 .4526 2.34 1.08 1.73 01
01 00 00 00 01 00 00 01 00 00 00
otu 049 04.0 30.0 00.0 5.0 6.0 03.0 05.0 01.0 00.0 07.0 00.0
01.0 01.0 02.0 5.0 3.0 4.0 7.0 4.8 1.3 00.0 6.2 2.5 6.0 11.5 41.0 07.0
05.0 19.0 1.46 8.79 9.0 1.08 1.27 1.03 .3283 3.12 1.26 2.46 01
01 01 01 00 00 00 00 01 01 00 00
otu 050 04.0 29.0 00.0 7.0 6.0 04.0 04.0 01.0 01.0 14.0 00.0
03.0 00.0 01.0 5.0 3.0 999. 999. 5.5 1.5 00.0 6.0 2.5 5.5 10.0 58.0 999.
06.0 16.0 1.70 9.64 31.0 1.03 1.33 1.81 .5747 3.14 1.33 2.36 01
01 01 01 00 00 00 00 01 00 00 00
otu 051 01.0 20.0 00.0 5.0 6.0 2.5 03.0 01.0 01.0 07.0 00.0
01.0 00.0 00.0 4.0 2.0 5.0 9.0 6.0 1.6 00.0 7.0 2.5 6.5 10.0 53.0 08.0
05.0 16.0 0.910 3.79 135.0 1.17 0.714 0.551 .3985 1.38 1.12 1.93 01
01 01 01 00 00 00 00 01 01 00 00
otu 052 01.0 30.0 00.0 3.0 3.0 04.0 04.0 01.0 00.0 09.0 00.0
03.0 00.0 00.0 3.5 2.0 5.0 7.0 3.8 1.3 00.0 5.0 2.2 5.0 7.8 29.0 07.0
04.0 14.0 1.53 7.63 22.0 1.01 1.14 1.26 .3729 3.37 1.03 2.96 999
999 999 999 999 999 999 999 999 999 999 999
otu 053 00.0 41.0 00.0 0.0 4.0 5.0 04.0 01.0 00.0 05.0 00.0
03.0 00.0 00.0 6.0 2.0 6.0 9.0 4.2 1.5 00.0 6.5 2.5 7.0 13.5 44.0 08.0
06.0 13.0 1.45 6.55 26.0 1.17 1.08 1.03 .3608 2.84 1.04 2.63 01
00 00 00 00 01 00 01 00 00 00 00
otu 054 01.0 16.0 00.0 7.0 7.0 3.3 05.0 00.0 00.0 08.0 00.0
01.0 00.0 01.0 5.7 2.0 6.0 10.0 5.5 1.7 00.0 6.0 2.5 6.0 11.0 61.0 09.0
05.0 18.0 1.28 7.45 158.0 1.22 1.73 1.03 .6363 1.62 1.47 0.94 00
01 00 00 01 00 01 00 00 00 00 00
otu 055 01.0 30.0 00.0 0.0 7.0 05.0 04.0 01.0 00.0 08.0 00.0
01.0 00.0 00.0 6.0 1.8 3.2 7.0 5.5 1.7 00.0 5.7 2.8 5.5 11.0 21.0 06.0
09.0 13.0 1.21 5.82 22.0 1.03 0.954 0.966 .4300 2.25 1.12 2.36 01
01 01 01 00 00 01 00 00 00 00 00
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01.0 00.0 00.0 5.0 2.0 4.0 9.0 4.5 1.7 00.0 5.0 2.1 5.6 11.0 39.0 07.0
04.0 14.0 1.75 6.97 66.0 1.15 1.61 1.45 .5888 2.46 1.11 1.53 01
01 01 01 00 00 01 00 00 00 00 00
otu 057 01.0 21.0 00.0 4.0 7.0 2.5 03.0 01.0 01.0 20.0 00.0
02.0 00.0 00.0 7.0 2.2 4.5 6.3 5.5 2.8 00.0 6.4 2.7 6.0 10.0 28.0 05.0
7.3 12.0 1.31 5.36 62.0 1.09 1.25 0.874 .4510 1.94 1.07 1.55 01
01 01 01 00 00 01 00 00 00 00 00
otu 058 01.0 30.0 00.0 00.0 7.0 2.0 02.0 01.0 00.0 16.0 01.0

01.0 00.0 00.0 06.0 02.5 999 5.5 04.5 999 0.0 5.5 02.4 999 08.0 26.0 09.0
05.0 13.0 01.77 08.02 999 1.060 01.49 0.690 0.227 3.06 1 07 2.05 999
999 999 999 999 999 999 999 999 999 999 999
otu 059 01.0 27.0 00.0 00.0 7.0 05.0 05.0 01.0 00.0 10.0 00.0
01.0 00.0 00.0 06.0 02.0 999 9.0 04.5 999 0.0 06.0 03.0 999 09.0 39.0 999
05.0 16.0 02.73 12.94 35.00 01.03 2.460 1.800 .3720 04.84 1.11 1.97 999
999 999 999 999 999 999 999 999 999 999 999
otu 060 04.0 27.0 00.0 00.0 6.0 03.2 02.0 01.0 00.0 29.0 01.0
02.0 00.0 00.0 06.0 03.8 999 06.0 05.5 999 0.0 6.2 03.2 999 10.0 20.0 999
06.0 14.0 01.59 06.82 41.00 1.130 01.30 00.91 .3380 02.70 1.07 2.08 999
999 999 999 999 999 999 999 999 999 999 999
otu 061 01.0 21.5 01.0 09.0 07.0 03.5 02.0 01.0 01.0 09.0 02.0
05.0 00.0 00.0 08.0 03.0 999 09.0 05.5 999 00.0 06.0 02.5 999 09.0 41.0 999
08.0 15.0 01.87 12.67 019.0 0.831 01.87 1.720 .4860 03.54 1.51 1.89 999
999 999 999 999 999 999 999 999 999 999 999
otu 062 01.0 33.5 00.0 05.0 6.0 06.0 06.0 01.0 01.0 18.0 02.0
01.0 00.0 00.0 06.0 02.5 999 10.0 04.0 999 0.0 05.5 02.2 999 09.0 25.0 06.0
06.0 13.0 02.06 10.38 15.00 00.98 02.18 01.08 .3500 03.08 1.28 1.41 999
999 999 999 999 999 999 999 999 999 999 999
otu 063 01.0 64.0 00.0 09.0 8.0 9.5 04.0 01.0 01.0 14.0 02.0
01.0 00.0 00.0 07.0 02.5 999 11.0 05.0 999 0.0 7.0 3.2 999 11.3 41.0 999
05.5 16.0 03.21 18.89 069.0 0.849 03.47 01.80 .4120 04.37 1.35 1.26 999
999 999 999 999 999 999 999 999 999 999 999
otu 064 999.41.0 00.0 08.0 07.0 5.8 07.0 01.0 01.0 14.0 02.0
01.0 00.0 00.0 06.0 2.5 999 08.0 6.0 999 00.0 6.5 3.0 999 10.0 34.0 999
06.0 14.0 01.84 08.33 049.0 1.060 02.03 01.15 .4570 02.53 01.2 1.25 999
999 999 999 999 999 999 999 999 999 999 999
otu 065 00.5 37.0 00.0 05.0 5.0 6.5 04.0 01.0 00.5 20.0 09.0
02.0 00.0 00.0 07.0 03.0 999 10.0 06.0 999 00.0 6.2 3.0 999 11.0 26.0 05.0
05.0 13.0 01.51 06.74 999 00.99 01.48 00.86 .3490 02.45 1.12 1.66 999
999 999 999 999 999 999 999 999 999 999 999
otu 066 01.0 57.0 00.0 05.0 06.0 7.5 07.0 01.0 01.0 12.0 02.0
01.0 00.0 00.0 05.5 02.0 999 10.0 06.0 999 00.0 07.0 3.2 999 11.2 27.0 999
05.5 13.0 01.97 09.56 013.0 00.95 01.87 01.95 .5130 03.79 1.08 2.03 999
999 999 999 999 999 999 999 999 999 999 999
otu 067 01.0 9.5 00.0 05.0 07.0 2.8 02.0 00.0 00.5 05.0 00.0
01.0 00.0 00.0 06.0 03.0 999 11.0 03.5 999 00.0 04.2 2.0 999 08.7 59.0 10.0
04.5 21.0 00.86 03.30 114.0 01.04 01.01 00.56 0.561 00.99 1.06 0.98 999
999 999 999 999 999 999 999 999 999 999 999
otu 068 01.0 08.5 00.0 06.0 07.0 1.7 02.0 01.0 00.0 03.0 00.0
01.0 00.0 00.0 07.0 03.0 999 12.0 03.2 999 00.0 05.0 2.0 999 08.8 72.0 14.0
05.0 20.0 01.60 06.94 63.00 01.01 01.74 01.02 0.495 02.05 1.15 1.18 999
999 999 999 999 999 999 999 999 999 999 999
otu 069 04.0 10.2 00.0 01.0 07.0 2.0 02.0 00.5 00.0 04.0 00.0
01.0 00.0 00.0 05.0 03.0 999 11.0 03.7 999 00.0 04.6 2.5 999 09.0 60.0 10.0
05.0 20.0 01.25 04.85 86.00 01.12 01.29 00.64 0.405 01.59 1.08 1.23 999

999 999 999 999 999 999 999 999 999 999 999
otu 070 01.0 36.0 01.0 05.0 06.0 5.2 04.0 01.0 00.5 11.0 04.0
03.0 03.0 01.0 06.0 02.0 999 11.0 04.5 999 00.0 06.5 2.5 999 12.0 50.0 07.0
04.5 21.0 02.77 12.30 56.00 01.06 02.90 01.69 0.444 03.82 1.20 1.31 01
01 01 00 00 00 00 00 00 01 00 00
otu 071 01.0 30.5 01.0 05.0 06.0 3.8 03.0 00.5 00.5 06.0 02.0
01.0 01.0 03.0 06.0 03.0 999 10.0 04.0 999 00.0 05.5 2.8 999 10.0 46.0 12.0
04.8 16.0 02.00 10.97 33.00 01.06 01.79 01.14 0.334 03.40 1.35 1.90 999
999 999 999 999 999 999 999 999 999 999 999
otu 072 01.0 32.0 01.0 05.0 05.0 5.0 03.0 01.0 00.0 05.0 01.0
01.0 01.0 03.0 05.0 03.0 999 11.0 04.5 999 00.0 05.2 3.0 999 08.0 22.0 999
04.2 12.0 02.59 13.00 27.00 01.12 02.28 01.79 0.448 03.98 1.32 1.74 01
01 01 00 00 00 00 00 00 01 00 00
otu 073 01.0 28.5 01.0 05.0 05.0 4.0 04.0 01.0 00.0 07.0 00.0
01.0 01.0 02.0 06.0 04.0 999 11.0 04.0 999 00.0 06.0 2.0 999 08.0 31.0 999
05.0 13.0 01.39 06.93 35.00 01.04 01.10 01.18 0.435 02.70 1.14 2.47 999
999 999 999 999 999 999 999 999 999 999 999
otu 074 04.0 36.0 00.0 05.0 06.0 5.0 04.0 00.5 01.0 09.0 01.0
01.0 00.0 00.0 07.0 03.0 999 10.0 04.0 999 00.0 05.0 2.0 999 999 63.0 05.0
06.0 15.0 02.11 09.68 31.00 01.10 01.51 02.22 0.505 04.40 1.01 2.91 999
999 999 999 999 999 999 999 999 999 999 999
otu 075 01.0 31.0 00.0 00.0 04.0 8.5 02.0 01.0 00.0 03.0 00.0
06.0 00.0 00.0 06.0 04.0 999 10.0 04.0 999 00.0 06.0 2.3 999 999 999 999
05.0 23.0 02.57 10.78 29.00 01.14 02.17 02.07 0.443 04.66 1.02 2.15 999
999 999 999 999 999 999 999 999 999 999 999
otu 076 999 57.0 00.0 09.0 08.0 11.0 02.0 01.0 01.0 12.0 03.0
01.0 00.0 00.0 06.0 04.0 999 11.0 04.1 999 00.0 05.5 2.2 999 08.0 66.0 11.0
05.0 23.0 02.20 21.23 58.00 00.78 01.35 02.85 0.489 05.83 1.56 4.32 999
999 999 999 999 999 999 999 999 999 999 999
otu 077 03.0 33.0 00.0 07.0 05.0 04.0 04.0 01.0 01.0 14.0 02.0
01.0 00.0 00.0 05.0 03.0 999 11.0 04.0 999 00.0 05.0 02.0 999 999 68.0 999
04.1 17.0 01.68 06.51 74.00 01.23 01.39 01.41 0.536 02.62 1.04 1.89 999
999 999 999 999 999 999 999 999 999 999 999
otu 078 00.5 26.5 00.0 03.0 04.0 04.4 03.0 01.0 01.0 08.0 00.0
01.0 00.0 00.0 06.0 02.0 999 999 999 999 999 06.0 02.3 999 999 999 999
05.0 15.0 02.72 11.04 139.0 01.36 03.38 01.46 0.415 03.51 1.09 1.04 999
999 999 999 999 999 999 999 999 999 999 999
otu 079 01.0 07.0 01.0 00.0 00.0 01.8 01.0 01.0 00.0 15.0 00.0
01.0 00.0 00.0 05.0 02.0 999 06.0 999 999 999 999 999 999 999 999 999
999 999 00.84 03.46 42.00 01.09 00.71 00.54 0.380 01.42 1.03 1.99 999
999 999 999 999 999 999 999 999 999 999 999
otu 080 01.0 32.0 00.0 05.0 05.0 05.2 03.0 00.5 00.0 14.0 00.0
01.0 00.0 00.0 06.0 02.0 999 11.0 04.3 999 0.00 05.2 02.5 999 09.0 30.0 999
05.1 13.0 999 999 999 999 999 999 999 999 999 999
999 999 999 999 999 999 999 999 999 999 999
otu 081 00.5 29.5 00.0 07.5 07.5 06.3 04.0 01.0 01.0 12.0 01.0

01.0 00.0 00.0 06.0 04.0 999 11.0 03.4 999 999 999 999 999 06.0
999 999 999 999 01.75 07.10 237.0 01.19 02.02 01.31 0.759 01.72 1.14 0.85 999
999 999 999 999 999 999 999 999 999 999 999
otu 082 01.0 999 00.0 09.0 09.0 05.0 08.0 00.5 01.0 999 01.0
01.0 00.0 03.0 07.0 03.0 999 12.0 04.0 999 999 05.5 02.5 999 999
999 999 999 15.0 999 999 77.00 00.87 999 999 0.556 999 1.14 3.23 999
999 999 999 999 999 999 999 999 999 999 999
otu 083 00.5 27.8 00.0 01.0 05.0 999 05.0 01.0 01.0 11.0 03.0
01.0 00.0 00.0 09.0 02.0 999 08.0 04.5 999 999 999 03.2 999 08.3
999 999 999 11.0 999 11.51 13.00 00.96 01.78 01.04 0.279 03.73 1.32 2.09 999
999 999 999 999 999 999 999 999 999 999 999
otu 084 999 30.0 00.0 01.0 05.0 06.0 02.0 01.0 00.0 01.0 01.0
01.0 00.0 00.0 07.0 02.0 999 11.0 999 999 999 06.0 02.5 999 999
999 999 999 999 01.98 10.39 53.00 01.02 02.34 01.25 0.468 02.67 1.39 1.14 999
999 999 999 999 999 999 999 999 999 999 999
otu 085 01.0 20.8 00.0 00.0 05.0 03.0 02.0 01.0 00.0 03.0 00.0
01.0 00.0 00.0 06.5 03.0 999 10.0 999 999 999 07.0 03.0 999 999
999 999 999 999 01.61 10.17 19.00 01.08 01.96 01.13 0.412 02.73 1.45 1.39 999
999 999 999 999 999 999 999 999 999 999 999
otu 086 999 30.8 00.0 00.0 05.0 06.0 02.0 01.0 01.0 04.0 03.0
01.0 00.0 00.0 07.0 02.0 999 07.0 999 999 999 06.0 02.3 999 14.5
999 999 999 999 01.80 19.16 149.0 01.23 02.94 01.68 0.556 03.01 2.19 1.02 999
999 999 999 999 999 999 999 999 999 999 999
otu 087 999 32.0 00.0 05.0 07.0 05.5 03.0 01.0 00.5 12.0 01.0
03.0 00.0 00.0 04.5 02.0 999 10.0 999 999 999 999 999 999 999
999 999 999 999 999 999 999 999 999 999 999 999 999 999 999 999
999 999 999 999 999 999 999 999 999 999 999
otu 088 01.0 27.5 00.0 05.0 06.0 05.6 03.0 01.0 00.5 07.0 00.0
01.0 00.0 00.0 07.5 02.0 999 09.0 999 999 999 06.5 03.0 999 07.5
999 999 999 999 01.90 10.31 101.0 00.95 01.88 01.47 0.490 03.01 1.35 1.60 999
999 999 999 999 999 999 999 999 999 999 999
otu 089 01.0 15.3 00.0 08.0 07.0 01.4 02.0 00.0 01.0 01.0 02.0
02.0 00.0 03.0 09.7 04.2 999 999 999 999 999 999 999 999 999
999 999 999 999 999 999 117.0 01.18 999 999 0.467 999 1.04 1.38 999
999 999 999 999 999 999 999 999 999 999 999
otu 090 04.0 28.0 00.0 01.0 01.0 07.5 04.0 01.0 01.0 09.0 0.00
01.0 00.0 00.0 06.0 03.0 999 09.0 03.2 999 00.0 04.0 02.2 999 999 65.0 09.0
04.5 21.00 14.24 8.04 45.00 01.08 02.14 04.70 0.450 03.17 1.02 1.48 00
01 00 00 01 01 01 00 00 00 00 01
otu 091 999 35.0 01.0 00.0 00.0 08.5 04.0 00.5 01.0 11.0 01.0
01.0 00.0 00.0 06.0 02.0 999 06.0 02.5 999 00.0 05.5 02.2 999 999 47.0 999
04.5 17.0 14.03 08.30 49.00 01.20 01.65 05.77 0.506 03.46 1.03 2.09 00
01 00 00 01 01 01 00 00 00 00 01
otu 092 03.0 43.0 00.0 01.0 00.5 07.0 03.0 01.0 00.5 08.0 02.0
01.0 00.0 00.0 06.0 03.0 999 09.0 04.2 999 00.0 05.0 02.1 999 10.1 45.0 06.0
06.0 17.0 13.64 09.15 27.00 01.17 01.45 05.66 0.428 04.01 1.03 2.77 00

01 00 00 01 01 01 00 00 00 00 01
otu 093 03.0 32.7 01.0 01.0 01.0 05.3 02.0 00.5 01.0 10.0 02.0
01.0 00.0 02.0 07.0 03.0 999 12.0 02.7 999 00.0 03.5 01.8 999 999 69.0 14.0
04.5 19.0 06.97 06.28 49.00 01.20 02.14 04.70 0.450 03.17 1.02 1.48 00
01 00 00 01 01 01 00 00 00 00 01
otu 094 02.0 15.0 00.0 05.0 06.0 01.8 03.0 01.0 00.0 06.0 00.0
01.0 00.0 00.0 07.0 03.0 999 09.0 05.0 999 00.0 05.5 02.1 999 07.5 39.0 999
04.2 13.0 08.08 05.85 93.00 01.27 01.65 02.33 0.370 01.91 1.08 1.16 00
01 00 00 01 00 01 00 00 00 00 00
otu 095 04.0 13.5 00.0 00.0 02.0 01.9 02.0 01.0 00.5 05.0 01.0
01.0 00.0 00.0 06.0 03.0 999 11.0 04.0 999 00.0 04.7 02.2 999 09.3 57.0 09.0
06.0 20.0 05.92 05.11 100.0 01.19 01.68 02.29 0.535 01.30 1.10 0.77 00
01 00 00 01 00 01 00 00 00 00 00
otu 096 03.0 15.0 00.0 02.0 05.0 02.6 02.0 01.0 01.0 06.0 00.0
01.0 00.0 00.0 06.0 03.0 999 11.0 04.3 999 00.0 05.7 02.2 999 11.0 56.0 10.0
05.0 18.0 04.82 04.41 95.00 01.21 01.29 02.42 0.482 01.52 1.04 1.18 00
01 00 00 01 00 01 00 00 00 00 00
otu 097 01.0 25.0 00.0 01.0 07.0 04.5 03.0 01.0 01.0 04.0 00.0
02.0 00.0 00.0 06.0 02.0 999 10.0 05.0 999 00.0 06.0 02.2 999 08.5 64.0 09.0
05.0 17.0 04.33 04.15 143.0 01.19 01.26 02.24 0.514 01.32 1.06 1.05 00
01 00 00 01 00 01 00 00 00 00 00

Appendix 3 - Descriptive statistics for 32 structural characters.

VARIABLE	N	MINIMUM	MAXIMUM	MEAN	STD DEV	
1.ROOT TYPE	6	1.0000	1.0000	1.0000		S. strept.
1.ROOT TYPE	18	0.	4.0000	.91667	.86177	var.borealis
1.ROOT TYPE	10	0.	3.0000	.90000	.90676	var.rubricaulis
1.ROOT TYPE	9	0.	4.0000	2.2222	1.5635	S. wallowensis
1.ROOT TYPE	4	1.0000	4.0000	2.7500	1.2583	S. laetiflorus
1.ROOT TYPE	8	.50000	1.5000	1.0000	.26726	S. oodes
1.ROOT TYPE	3	1.0000	4.0000	3.0000	1.7321	S. kluanei
2.STALK HT.	6	20.000	38.000	28.000	6.8411	S. strept.
2.STALK HT.	18	22.500	47.000	29.611	6.3514	var.borealis
2.STALK HT.	11	26.300	64.000	41.709	11.353	var.rubricaulis
2.STALK HT.	9	8.5000	36.000	17.244	9.0118	S. wallowensis
2.STALK HT.	6	28.000	62.000	42.950	13.799	S. laetiflorus
2.STALK HT.	8	15.000	43.000	31.938	8.3642	S. oodes
2.STALK HT.	3	14.500	30.000	24.500	8.6747	S. kluanei
3.LF. PUBESCENCE	6	0.	0.	0.		S. strept.
3.LF. PUBESCENCE	18	0.	1.0000	.55556 -1	.23570	var.borealis
3.LF. PUBESCENCE	11	0.	0.	0.		var.rubricaulis
3.LF. PUBESCENCE	9	0.	0.	0.		S. wallowensis
3.LF. PUBESCENCE	6	0.	1.0000	.33333	.51640	S. laetiflorus
3.LF. PUBESCENCE	8	1.0000	3.0000	1.5000	.75593	S. oodes
3.LF. PUBESCENCE	3	0.	2.0000	.66667	1.1547	S. kluanei
4.LWR. LF. MAR.	6	0.	4.0000	1.3333	2.0656	S. strept.
4.LWR. LF. MAR.	18	0.	3.0000	.38889	.91644	var.borealis
4.LWR. LF. MAR.	11	4.0000	9.0000	7.2727	2.0538	var.rubricaulis
4.LWR. LF. MAR.	9	0.	6.0000	2.8889	2.3154	S. wallowensis
4.LWR. LF. MAR.	6	0.	10.000	3.6667	4.5461	S. laetiflorus
4.LWR. LF. MAR.	8	1.0000	7.0000	5.0000	1.8516	S. oodes
4.LWR. LF. MAR.	3	0.	7.0000	4.0000	3.6056	S. kluanei
5.UPP. LF. MAR.	6	4.0000	7.0000	6.0000	1.5492	S. strept.
5.UPP. LF. MAR.	18	3.0000	7.0000	5.0000	1.7489	var.borealis
5.UPP. LF. MAR.	11	4.0000	9.0000	6.2727	1.6787	var.rubricaulis
5.UPP. LF. MAR.	9	2.0000	7.0000	6.0000	1.6583	S. wallowensis
5.UPP. LF. MAR.	6	0.	8.0000	2.9167	3.5835	S. laetiflorus
5.UPP. LF. MAR.	8	4.0000	7.0000	5.7500	1.0351	S. oodes
5.UPP. LF. MAR.	3	6.0000	7.0000	6.3333	.57735	S. kluanei
6.PETIOLE L.	6	2.1000	5.0000	3.9667	1.3337	S. strept.
6.PETIOLE L.	18	2.0000	8.5000	3.7000	1.5945	var.borealis
6.PETIOLE L.	11	1.8000	9.5000	5.6182	2.3609	var.rubricaulis
6.PETIOLE L.	9	1.7000	5.0000	2.8111	1.1973	S. wallowensis
6.PETIOLE L.	6	5.3000	11.000	7.9167	1.8862	S. laetiflorus
6.PETIOLE L.	8	2.2000	9.0000	4.5875	2.1115	S. oodes
6.PETIOLE L.	3	2.2000	4.0000	3.0667	.90185	S. kluanei
7.CAUL. LF. #	6	3.0000	8.0000	4.5000	1.8708	S. strept.
7.CAUL. LF. #	18	2.0000	9.0000	4.5000	2.0073	var.borealis

7.CAUL. LF. #	11	3.0000	7.0000	5.1818	1.4709		var.rubricaulis
7.CAUL. LF. #	9	2.0000	4.0000	2.5556	.72648	S.	wallowensis
7.CAUL. LF. #	6	2.0000	5.0000	3.3333	1.2111	S.	laetiflorus
7.CAUL. LF. #	8	2.0000	6.0000	3.8750	1.2464	S.	oodes
7.CAUL. LF. #	3	1.0000	5.0000	3.3333	2.0817	S.	kluanei
8.CAUL. LF. BASE	6	1.0000	1.0000	1.0000		S.	strept.
8.CAUL. LF. BASE	18	0.	1.0000	.83333	.38348		var.borealis
8.CAUL. LF. BASE	11	0.	1.0000	.90909	.30151		var.rubricaulis
8.CAUL. LF. BASE	9	0.	1.0000	.77778	.36324	S.	wallowensis
8.CAUL. LF. BASE	1	0.	1.0000	.66667	.40825	S.	laetiflorus
8.CAUL. LF. BASE	8	.50000	1.0000	.93750	.17678	S.	oodes
8.CAUL. LF. BASE	3	1.0000	1.0000	1.0000		S.	kluanei
9.CAUL. LF. MAR.	6	0.	1.0000	.33333	.51640	S.	strept.
9.CAUL. LF. MAR.	18	0.	1.0000	.55556 -1	.23570		var.borealis
9.CAUL. LF. MAR.	11	.50000	1.0000	.95455	.15076		var.rubricaulis
9.CAUL. LF. MAR.	9	0.	1.0000	.44444	.46398	S.	wallowensis
9.CAUL. LF. MAR.	6	.50000	1.0000	.91667	.20412	S.	laetiflorus
9.CAUL. LF. MAR.	8	0.	1.0000	.25000	.37796	S.	oodes
9.CAUL. LF. MAR.	3	0.	1.0000	.33333	.57735	S.	kluanei
10.HD #	6	5.0000	20.000	12.500	5.7533	S.	strept.
10.HD #	18	3.0000	35.000	14.111	8.2952		var.borealis
10.HD #	11	7.0000	20.000	13.818	3.8683		var.rubricaulis
10.HD #	9	3.0000	9.0000	5.6667	2.1213	S.	wallowensis
10.HD #	6	8.0000	12.000	9.8333	1.4720	S.	laetiflorus
10.HD #	8	5.0000	11.000	8.5000	2.3299	S.	oodes
10.HD #	3	5.0000	14.000	8.6667	4.7258	S.	kluanei
11.SEC. STALKS	6	0.	3.0000	.50000	1.2247	S.	strept.
11.SEC. STALKS	18	0.	3.0000	.50000	.85749		var.borealis
11.SEC. STALKS	11	0.	9.0000	1.9091	2.5082		var.rubricaulis
11.SEC. STALKS	9	0.	1.0000	.22222	.44096	S.	wallowensis
11.SEC. STALKS	6	0.	3.0000	1.8333	1.1690	S.	laetiflorus
11.SEC. STALKS	8	0.	4.0000	.87500	1.4577	S.	oodes
11.SEC. STALKS	3	0.	0.	0.		S.	kluanei
12.STALK #	6	1.0000	2.0000	1.1667	.40825	S.	strept.
12.STALK #	18	1.0000	6.0000	2.0556	1.6968		var.borealis
12.STALK #	11	1.0000	2.0000	1.2727	.46710		var.rubricaulis
12.STALK #	9	1.0000	2.0000	1.1111	.33333	S.	wallowensis
12.STALK #	6	1.0000	2.0000	1.1667	.40825	S.	laetiflorus
12.STALK #	8	1.0000	3.0000	1.2500	.70711	S.	oodes
12.STALK #	3	1.0000	3.0000	1.6667	1.1547	S.	kluanei
13.UPP. INV PUB	6	0.	0.	0.		S.	strept.
13.UPP. INV PUB	8	0.	1.0000	.11111	.32338		var.borealis
13.UPP. INV PUB	1	0.	0.	0.			var.rubricaulis
13.UPP. INV PUB	9	0.	0.	0.		S.	wallowensis
13.UPP. INV PUB	6	0.	1.0000	.16667	.40825	S.	laetiflorus
13.UPP. INV PUB	8	0.	3.0000	1.2500	.88641	S.	oodes

13.UPP. INV PUB	3	0.	2.0000	1.0000	1.0000	S. kluanei
14.LWR. INV PUB	6	0.	0.	0.		S. strept.
14.LWR. INV PUB	8	0.	1.0000	.11111	.32338	var.borealis
14.LWR. INV PUB	1	0.	0.	0.		var.rubricaulis
14.LWR. INV PUB	9	0.	0.	0.		S. wallowensis
14.LWR. INV PUB	6	0.	2.0000	.50000	.83666	S. laetiflorus
14.LWR. INV PUB	8	1.0000	3.0000	2.6250	.74402	S. oodes
14.LWR. INV PUB	3	1.0000	3.0000	2.0000	1.0000	S. kluanei
15.INV L.	6	5.0000	7.0000	6.3333	.81650	S. strept.
15.INV L.	18	3.5000	6.0000	5.1611	.83182	var.borealis
15.INV L.	11	4.0000	7.0000	5.8636	.83937	var.rubricaulis
15.INV L.	9	4.2000	7.0000	6.0222	.95102	S. wallowensis
15.INV L.	6	6.0000	7.0000	6.1667	.40825	S. laetiflorus
15.INV L.	8	4.0000	6.0000	5.3750	.74402	S. oodes
15.INV L.	3	5.0000	5.0000	5.0000		S. kluanei
16.INV W.-BASE	6	1.8000	4.0000	2.3333	.82624	S. strept.
16.INV W.-BASE	18	2.0000	4.0000	2.4833	.67932	var.borealis
16.INV W.-BASE	11	1.5000	3.0000	2.4364	.50452	var.rubricaulis
16.INV W.-BASE	9	2.0000	3.0000	2.7778	.44096	S. wallowensis
16.INV W.-BASE	6	2.0000	5.0000	3.3333	1.0328	S. laetiflorus
16.INV W.-BASE	8	2.0000	4.0000	2.7500	.70711	S. oodes
16.INV W.-BASE	3	2.0000	3.0000	2.6667	.57735	S. kluanei
17.HD. DIA.	5	6.3000	9.0000	7.6600	1.0383	S. strept.
17.HD. DIA.	18	5.5000	11.000	8.3611	1.6342	var.borealis
17.HD. DIA.	11	7.0000	11.000	9.3636	1.2863	var.rubricaulis
17.HD. DIA.	9	6.0000	12.000	10.111	1.7638	S. wallowensis
17.HD. DIA.	6	6.0000	12.000	9.6667	2.1602	S. laetiflorus
17.HD. DIA.	8	7.5000	11.000	9.4375	1.4985	S. oodes
17.HD. DIA.	2	7.0000	8.0000	7.5000	.70711	S. kluanei
18.PAPP. L.	6	3.7000	6.0000	5.0333	.82865	S. strept.
18.PAPP. L.	18	3.0000	6.5000	4.6111	.83376	var.borealis
18.PAPP. L.	11	4.0000	6.0000	5.2727	.87646	var.rubricaulis
18.PAPP. L.	9	3.2000	5.0000	4.1889	.68455	S. wallowensis
18.PAPP. L.	6	2.5000	6.0000	3.7833	1.2922	S. laetiflorus
18.PAPP. L.	8	4.0000	5.0000	4.4625	.39256	S. oodes
18.PAPP. L.	3	4.0000	5.5000	4.7667	.75056	S. kluanei
19.DISC L.	6	5.3000	6.4000	5.8167	.39707	S. strept.
19.DISC L.	18	4.0000	6.5000	5.6667	.68083	var.borealis
19.DISC L.	11	5.5000	8.0000	6.5182	.67204	var.rubricaulis
19.DISC L.	9	4.2000	6.0000	5.0778	.56740	S. wallowensis
19.DISC L.	6	3.5000	5.5000	4.8167	.86120	S. laetiflorus
19.DISC L.	8	5.2000	6.5000	6.0000	.45981	S. oodes
19.DISC L.	3	5.8000	6.2000	6.0000	.20000	S. kluanei
20.ANTH. L.	6	2.2000	3.0000	2.7000	.30984	S. strept.
20.ANTH. L.	18	1.8000	2.8000	2.3389	.29132	var.borealis
20.ANTH. L.	11	2.2000	3.2000	2.9000	.31305	var.rubricaulis

20.ANTH. L.	9	2.0000	2.5000	2.1667	.16583	S. wallowensis
20.ANTH. L.	6	1.8000	2.5000	2.1667	.22509	S. laetiflorus
20.ANTH. L.	8	2.0000	3.0000	2.4625	.38149	S. oodes
20.ANTH. L.	3	2.5000	2.8000	2.6000	.17321	S. kluanei
21.RAY L.	5	9.0000	11.000	10.400	.89443	S. strept.
21.RAY L.	16	7.5000	13.500	9.2875	1.6713	var.borealis
21.RAY L.	11	8.0000	14.000	10.618	1.7600	var.rubricaulis
21.RAY L.	8	7.5000	11.000	8.8250	1.0634	S. wallowensis
21.RAY L.	3	8.0000	11.700	9.9333	1.8556	S. laetiflorus
21.RAY L.	8	8.0000	12.000	9.4750	1.4059	S. oodes
21.RAY L.	3	7.0000	11.500	9.5000	2.2913	S. kluanei
22.DISC #	6	21.000	45.000	33.667	8.8468	S. strept.
22.DISC #	17	25.000	54.000	36.176	8.0018	var.borealis
22.DISC #	11	25.000	43.000	32.727	6.9439	var.rubricaulis
22.DISC #	9	39.000	72.000	57.889	9.1984	S. wallowensis
22.DISC #	6	45.000	96.000	64.667	18.446	S. laetiflorus
22.DISC #	8	22.000	63.000	40.750	13.477	S. oodes
22.DISC #	3	39.000	58.000	46.000	10.440	S. kluanei
23.RAY #	4	5.0000	10.000	7.2500	2.2174	S. strept.
23.RAY #	11	6.0000	10.000	7.8182	1.0787	var.borealis
23.RAY #	6	5.0000	10.000	7.3333	1.9664	var.rubricaulis
23.RAY #	7	5.0000	14.000	9.5714	2.6367	S. wallowensis
23.RAY #	5	6.0000	14.000	10.200	2.9496	S. laetiflorus
23.RAY #	4	7.0000	12.000	8.7500	2.2174	S. oodes
23.RAY #	2	6.0000	7.0000	6.5000	.70711	S. kluanei
24.PHYL. L.	6	5.0000	9.0000	6.3833	1.5368	S. strept.
24.PHYL. L.	18	4.0000	6.0000	4.8000	.50759	var.borealis
24.PHYL. L.	11	3.8000	6.0000	5.4364	.65920	var.rubricaulis
24.PHYL. L.	9	4.2000	6.0000	5.0000	.65000	S. wallowensis
24.PHYL. L.	6	4.5000	6.0000	5.0833	.73598	S. laetiflorus
24.PHYL. L.	8	4.2000	6.0000	4.9375	.52082	S. oodes
24.PHYL. L.	3	4.0000	6.0000	5.0000	1.0000	S. kluanei
25.PHYL. #	6	10.000	16.000	13.000	2.0000	S. strept.
25.PHYL. #	18	10.000	23.000	14.500	3.1854	var.borealis
25.PHYL. #	11	13.000	21.000	15.000	2.6077	var.rubricaulis
25.PHYL. #	9	13.000	21.000	17.556	2.9627	S. wallowensis
25.PHYL. #	6	17.000	23.000	19.667	2.4221	S. laetiflorus
25.PHYL. #	8	12.000	21.000	15.625	3.7773	S. oodes
25.PHYL. #	3	16.000	19.000	17.333	1.5275	S. kluanei
26.LF. PER.	6	4.0900	12.940	7.5217	3.8975	S. strept.
26.LF. PER.	18	4.9100	11.270	7.2006	1.8980	var.borealis
26.LF. PER.	11	6.7400	19.550	12.452	4.4000	var.rubricaulis
26.LF. PER.	9	3.3000	9.6800	5.4178	1.9070	S. wallowensis
26.LF. PER.	6	6.2800	21.230	11.842	6.1945	S. laetiflorus
26.LF. PER.	8	4.0700	13.980	9.7125	3.4084	S. oodes
26.LF. PER.	3	8.7900	19.800	12.743	6.1260	S. kluanei

27.LF. BASE	6	18.000	62.000	35.667	15.629		S. strept.
27.LF. BASE	17	7.0000	91.000	31.318	21.291		var.borealis
27.LF. BASE	10	13.000	142.00	60.500	46.748		var.rubricaulis
27.LF. BASE	9	31.000	143.00	87.000	32.955		S. wallowensis
27.LF. BASE	5	27.000	58.000	45.600	11.437		S. laetiflorus
27.LF. BASE	8	5.0000	56.000	33.125	15.707		S. oodes
27.LF. BASE	3	9.0000	31.000	19.000	11.136		S. kluanei
28.MX WIDTH	6	.92100	2.4600	1.4575	.63350		S. strept.
28.MX WIDTH	18	.69100	2.1700	1.2273	.38748		var.borealis
28.MX WIDTH	11	1.2200	3.4700	2.0282	.68585		var.rubricaulis
28.MX WIDTH	9	1.0100	1.7400	1.3933	.26177		S. wallowensis
28.MX WIDTH	6	1.3500	3.3400	2.0117	.73232		S. laetiflorus
28.MX WIDTH	8	.70000	2.9000	1.8087	.74838		S. oodes
28.MX WIDTH	3	.96600	1.3300	1.1887	.19515		S. kluanei
29.DIST. RATIO	6	.22850	.45100	.37160	.80754	-1	S. strept.
29.DIST. RATIO	18	.27600	-1 .49210	.32229	.13168		var.borealis
29.DIST. RATIO	11	.34900	.66210	.44468	.92480	-1	var.rubricaulis
29.DIST. RATIO	9	.37000	.56100	.47687	.63521	-1	S. wallowensis
29.DIST. RATIO	6	.42800	.52930	.47538	.38894	-1	S. laetfflorus
29.DIST. RATIO	8	.33400	.54760	.43280	.62432	-1	S. oodes
29.DIST. RATIO	3	.32830	.57470	.45293	.12323		S. kluanei
30.LF. LENGTH	6	1.8400	4.8400	2.9167	1.3733		S. strept.
30.LF. LENGTH	18	1.9300	4.7400	2.9922	.85051		var.borealis
30.LF. LENGTH	11	2.4500	4.4900	3.4736	.68219		var.rubricaulis
30.LF. LENGTH	9	.99000	4.4000	1.8533	1.0067		S. wallowensis
30.LF. LENGTH	6	3.1700	10.750	5.0650	2.9589		S. laetiflorus
30.LF. LENGTH	8	1.7400	3.9800	3.2787	.74721		S. oodes
30.LF. LENGTH	3	2.4000	3.1400	2.8867	.42158		S. kluanei
31.PER. RATIO	6	1.0200	1.1800	1.0917	.57067	-1	S. strept.
31.PER. RATIO	18	1.0200	1.0800	1.0489	.21113	-1	var.borealis
31.PER. RATIO	11	1.0800	1.8900	1.3827	.25378		var.rubricaulis
31.PER. RATIO	9	1.0100	1.1500	1.0756	.40035	-1	S. wallowensis
31.PER. RATIO	6	1.0200	1.6400	1.2167	.29804		S. laetiflorus
31.PER. RATIO	8	1.0300	1.4300	1.1962	.15454		S. oodes
31.PER. RATIO	3	1.0400	1.3300	1.2100	.15133		S. kluanei
32.L/W RATIO	6	1.5500	2.3600	2.0033	.35438		S. strept.
32.L/W RATIO	18	1.2400	3.6300	2.5594	.70097		var.borealis
32.L/W RATIO	11	1.2500	2.9700	1.8455	.60229		var.rubricaulis
32.L/W RATIO	9	.77000	2.9100	1.3222	.62313		S. wallowensis
32.L/W RATIO	6	1.4800	4.3200	2.5600	1.1073		S. laetiflorus
32.L/W RATIO	8	1.3100	2.5000	1.9700	.44407		S. oodes
32.L/W RATIO	3	2.3600	2.4800	2.4333	.64291	-1	S. kluanei

Appendix 4 - Representative Specimens

Senecio streptanthifolius Greene var. *streptanthifolius* Greene

BC: near Alta. border along hwy 3, 3 mi. W. of Coleman, *Taylor & Ferguson 808* (ORE); **BC:** Mt. Apex-SW of Penticton, *Calder & Savile 11715* (RM 256339, UC M290802); **BC:** Chilliwack valley, *Macoun 26679* (ND-G 062991, GH); **CALIFORNIA:** MONO CO: Sonora Pass - Sweetwater Mtns., *J. Bain 206* (ALTA); **CALIFORNIA:** NEVADA CO: Cisco trail, Red mtn, Tahoe NF, *Eggleston 21680* (US 1534313); **CALIFORNIA:** SHASTA CO: hdwaters of Hat cr, *Eggleston 7494* (NY, GH, US 623893); **CALIFORNIA:** SIERRA CO: Sierraville, *Hall & Babcock 4473* (GH, UC 53868); **COLORADO:** CUSTER CO: trail to Lake of Clouds, Sangre del Cristo range, W. of Westcliffe, *Weber 5895* (COLO 61538, MO 1600526); **COLORADO:** GUNNISON CO: 8.3 km W. of summit of Monarch Pass on roadside, Hwy 50, *J. Bain 101A* (ALTA); **COLORADO:** GUNNISON CO: N. Italian mtn, *Langenheim 388* (COLO 79378); **COLORADO:** GUNNISON CO: Upper Virginia Basin-SW slope, *Russell 4.9* (UC M183463); **COLORADO:** GUNNISON CO: 6.5 mi S Iola- btwn Nine mile hill & Willow cr., *Barrell 14-66* (US 2870923); **COLORADO:** HUERFANO CO: below Apishapa pass, *Barkley & Anderson 2448* (NY); **COLORADO:** SAGUACHE CO: S. of Los Pinos pass, *Barrell 653-62* (US 2870921); **IDAHO:** 8 km. N Ketchum, *Henderson 3234* (F 700281, MO 921503, US 233623 233625, NY); **IDAHO:** Beaver canyon, *Rydberg* (NY); **IDAHO:** Beaver canyon, *Shear 3028* (NY, US 835130); **IDAHO:** Beaver canyon, *Shear 3122* (NY); **IDAHO:** Beaver canyon, *Shear 4405* (NY); **IDAHO:** Little Dry cr canyon, nr stream banks, *Rust 677* (US 870516); **IDAHO:** BEAR L. CO: 10 mi W Bloomington, Bear R. range, *Baker 9376* (NY); **IDAHO:** BLAINE CO: Galena summit, *Baker 10682* (NY); **IDAHO:** BLAINE CO: Neal canyon above Ketchum, *M. Lewis 2690* (NY); **IDAHO:** BLAINE CO: Lost R. mtn, nr Clyde, *Macbride & Payson 3155* (NY, US 871152, MO 814832, GH ,

UC 256361); **IDAHO:** BLAINE CO: Boulder cr.canyon, Sawtooth NF, *JWThompson 14061* (F 946306, MO 1218217, GH, NY, US 1731407); **IDAHO:** BLAINE CO: Hyndman cr, *JWThompson 13509* (NY, MO 118325); **IDAHO:** BLAINE CO: near Martin, Antelope mtns, *Macbride & Payson 3062* (US 871121, MO 814829, GH); **IDAHO:** BLAINE CO: Norton pk, Smokey mtns, nr L. Norton L., *Hitchcock & Muhlick 10722* (NY); **IDAHO:** BLAINE CO: Big Wood R., 9 mi N of Ketchum, *Cronquist 2418* (MO 1212147, GH); **IDAHO:** BLAINE CO: Neal canyon above Ketchum, *Lewis 2690* (IM 136745); **IDAHO:** BOISE CO: above Sacajawea hot spgs-Sawtooth prim area, *Hitchcock&Muhlick 9885* (NY); **IDAHO:** CAMAS CO: 1 mi W summit-Ketchum-Featherville Rd., Soldier mtns, *Hitchcock & Muhlick 10421* (NY, CAN 195189, IM 66595, GH, UC 969264); **IDAHO:** CASSIA CO: Mt Harrison, *Davis 1330* (IM 61707, UC 829725); **IDAHO:** CLARK CO: 3 mi N of Spencer, along Beaver Cr., *Cronquist 1309* (MO 1183323, IM 38678); **IDAHO:** CLARK CO: Spencer L. -Dry cr canyon, *Christ 2844* (NY); **IDAHO:** CLARK CO: NW of Kilgore, top of cliff over W. Camas, *Cronquist 1392* (IM 38786, MO 1183324); **IDAHO:** CUSTER CO: 20 mi W. Challis, *Baker 10751* (NY); **IDAHO:** CUSTER CO: btwn Custer & Five Mile creek, *Cronquist 2882* (MO 1212145, GH); **IDAHO:** CUSTER CO: Challis NF.-hr Stanley, *JWThompson 14035* (F 946354, MO 1218182, GH); **IDAHO:** CUSTER CO: Bear cr., below Parker mtn, *Macbride & Payson 3307* (US 871210, MO 814830, GH , UC 256362, NY); **IDAHO:** CUSTER CO: N of camp F-83, Bonanza, *Smith 107* (IM 22286); **IDAHO:** CUSTER CO: 4 mi NE of Dickey canyon, *Cronquist 3130* (MO 1212146, GH); **IDAHO:** CUSTER CO: Cherry cr, *Davis 1264* (IM 60824); **IDAHO:** CUSTER CO: 1 mi W of Borah-hd of Rock creek, *Hitchcock & Muhlick 10990* (NY, IM 66664, UC 969220); **IDAHO:** CUSTER CO: Boulder cr at sawmill, *Cronquist 569* (NY); **IDAHO:** CUSTER CO: 11 mi N Bonanza, *Christ 15670* (NY); **IDAHO:** CUSTER CO: Lemhi range, W. Mt Mogg, *Hitchcock & Muhlick 11232* (GH, US 1923369, IM 66229, CAN 195190, NY, COLO 51932); **IDAHO:** FREMONT CO: Red rock pass, *Christ 5766* (NY); **IDAHO:** FRANKLIN CO: Bear R. range-2 mi W Franklin stn, *Maguire 21638* (IM 104997, NY, UC M249541); **IDAHO:** IDAHO CO: Seven devil guard stn, seven devils mtn, *Baker 12066* (NY); **IDAHO:** IDAHO CO: 1 mi E Seven devils

camp, *Christ 12511* (NY); **IDAHO:** IDAHO CO: Heavens gate, Seven devils mtn, *Christ 12520* (NY); **IDAHO:** IDAHO CO: Seven devils guard stn, S. D. mtns, *Baker 12066* (NY); **IDAHO:** LEMHI CO: 11 mi SE Baker, Warm spgs cr rd., *Bennett 7693* (F 1589680); **IDAHO:** LEMHI CO: Gilmore, *Christ & Ward 14846* (NY); **IDAHO:** LEMHI CO: U. Silver cr, *Lewis 2651* (IM 136778); **IDAHO:** LEMHI CO: Wm spgs Rd.–Pattee cr canyon, 11 mi SE Baker–mtns, *Bennett 7693* (IM 127804); **IDAHO:** OWYHEE CO: Three creek, *Nelson & Macbride 2247* (US 544977, GH); **IDAHO:** VALLEY CO: Thunderbolt mtn, Payette NF, Sawtooth mtns, *JWThompson 13926* (F 946122, IM 59776, US 1727725, GH, MO 1219145, NY); **MONTANA:** Duck L., *Weller* (US 411611); **MONTANA:** Little Belt pass, *Flodman 910* (US 290955, NY); **MONTANA:** BEAVERHEAD CO: Vipont park, E of Sheep mtn, *Hitchcock & Muhlick 13018* (IM 71241, MO 1295999, UC 757575); **MONTANA:** GRANITE CO: Rock cr canyon, – Eagle creek, *Hitchcock & Muhlick 14451* (MO 1302898); **MONTANA:** MEAGHER CO: 3.3 km S. of Cascade Co. line on Hwy #89, at King's Hill Pass, *J. Bain 109* (ALTA); **MONTANA:** MEAGHER CO: 3 mi W Harlowton, on W Sulphur spgs Rd., *Hitchcock & Muhlick 12069* (IM 70805); **NEVADA:** ELKO CO: Bear Cr. meadows, *Holmgren 1688* (BYU 28726, IM 48060, UC 676215); **NEVADA:** ELKO CO: Bear cr hdwtrs, *Train 715* (F 1484003, UC 831696); **NEVADA:** ELKO CO: 3.5 mi E N fk, *Holmgren 1879* (IM 48059); **NEVADA:** ELKO CO: Cottonwood drainage, Jarbidge wilderness, *Lewis & Walters 4547* (IM 151437); **NEVADA:** ELKO CO: 3 mi E of Montello, Ut–Nev st line, *Train 3748* (NY, IM 53356, UC 53356); **NEVADA:** ELKO CO: Lamoille canyon, *Lewis 1846* (IM 128405); **UTAH:** Salt L. city, *M.E. Jones 1996* (F 252611, US 227883); **UTAH:** below Silver L., Big Cottonwood canyon, *Rydberg & Carleton 6634* (NY); **UTAH:** CACHE CO: Mt. Naomi, *Maguire 16196* (BYU 45922, IM 119428, GH, NY); **UTAH:** CACHE CO: Bear R. range– nr summit Mt. Magog, *Maguire 14060* (IM 104993, NY); **UTAH:** CACHE CO: Saddle mtns., Naomi, *Maguire 14193* (IM 104996, NY); **UTAH:** CACHE CO: Mt Magog–White pine canyon, *Tillett 354* (IM 89388); **UTAH:** CACHE CO: NW slope Mt. Magog, *Maguire 14068* (IM 104992, NY); **UTAH:** EMERY CO: hd. Riddle canyon, Manti–Lasal NF, *Lewis 5157* (IM 151891, BYU 179144); **UTAH:** EMERY CO: flat

canyon E. of Joes valley, Manti-Lasal NF, *Lewis 4739* (IM 151267); **UTAH:** GARFIELD CO: 2 mi N Cyclone L.-Dixie NF- Aquarius plateau, *Maquire 19256* (NY); **UTAH:** JUAB CO: 15 mi cr, *McMillan 886* (IM 122251); **UTAH:** SAN PETE CO: S. of Tent mtn. Manti-lasal NF, *Lewis 4364* (IM 147592, BYU 168750); **UTAH:** SAN PETE CO: Manti-Lasal NF, *Birtic 294* (IM 140779); **UTAH:** SAN PETE CO: ridge to Musinia pk. Manti-lasal NF, *Lewis 5521* (IM 155802); **UTAH:** SAN PETE CO: *Maquire 20049a* (NY); **UTAH:** SAN PETE CO: above the cove Manti Lasal NF, *Lewis & Harper 6570* (BYU 220878); **UTAH:** SAN PETE CO: M. forks park, *Maguire 20045* (NY, IM 105035, GH); **UTAH:** SAN PETE CO: hd. 12 mi. canyon, Camel rock area, Manti-lasal NF, *Lewis 4275* (IM 150706); **UTAH:** SAN PETE CO: above the cove Manti-lasal NF, *Lewis 6570* (IM 166823); **UTAH:** SEVIER CO: hdwaters Fremont R., Wasatch, *Eggleston 10338* (US 767331); **UTAH:** WASATCH CO: nr Midway, *Carleton & Garrett 6701* (US 508617); **WASHINGTON:** CHELAN CO: wooded slopes of Mt. Stuart, *JWThompson 7641* (ORE, MO 1008888, GH, US 1565200); **WASHINGTON:** KITTITAS CO: above Ole Elum R., btwn Scatter and Silver Cr., *A.R.Kruckeberg 2999* (ORE); **WASHINGTON:** Mt Paddo(Mt Adams), *Suksdorf 73* (GH); **WASHINGTON:** Carson mtn.- Marble mtns, *JWThompson 14965* (MO 1201903, CAN 195188, IM 62654, GH, UC 749582, COLO 86186); **WASHINGTON:** Mt Stuart, *Sandberg & Leiberg* (ND-G 063263); **WASHINGTON:** Hd Pirsin creek, *Gorman 809* (US 303442); **WASHINGTON:** Cascade mtn., *Grant* (RM 117123); **WASHINGTON:** slopes Mt. Stuart, *Sandberg & Leiberg 553* (F 324520, MO 1719538, GH, UC 182904); **WASHINGTON:** CHELAN CO: Nigger cr, Wenatchee mtns, *JWThompson 8570* (ND-G 010488, RM 133006); **WASHINGTON:** CHELAN CO: along Nigger creek, *JWThompson 8579* (UC 831701); **WASHINGTON:** CHELAN CO: wooded slopes of Mt. Stuart, *JWThompson 7641* (ORE, MO 1008888, GH, US 1565200); **WASHINGTON:** CHELAN CO: hd. Falls Creek, near Bryan butte, *Ward 58* (COLO 72882); **WASHINGTON:** CHELAN CO: Three Bros pk, *JWThompson 12618* (ND-G 010494, MO 1205764, US 1650880, UC 832101); **WASHINGTON:** CHELAN CO: Mt. Stuart, *JWThompson 5831* (MO 991602, GH); **WASHINGTON:** CHELAN CO: Three brothers pk, *JWThompson 10568* (MO 1080440); **WASHINGTON:** KING CO: trail to Snow L.-Cascades, *JWThompson*

10642 (MO 1081500, US 1633389); **WASHINGTON:** KITTATAS CO: above Ole Elum River–between Scatter & Silver Creeks, *Kruckeberg 2999* (COLO 104014, UC M012901, RM 239276, ORE); **WASHINGTON:** KITTATAS CO: Mt. Stuart, *Elmer 1384* (MO 1719539); **WASHINGTON:** KITTATAS CO: Wanatchee Mtns.– Iron Creek Trail, approx. 10 mi. NNE of Cle Elum, *J. Bain 205* (ALTA); **WASHINGTON:** KITTATAS CO: 1 mi SW. Teanaway–Turnpike creek, *Kruckeberg 2607* (RM 232451, COLO 79559, UC 931445); **WASHINGTON:** KITTATAS CO: W. base Iron Pk., upper N. fork Teanaway River, *Kruckeberg 2582* (RM 232414, UC 931611, COLO 87960); **WASHINGTON:** KITTATAS CO: Beverly cr hd, *JWThompson 9502* (ND–G 010497, US–G 1419747, MO 1064397, GH, UC 518186); **WASHINGTON:** KITTATAS CO: Bald mtn, *JWThompson 14852* (MO 1201922, GH); **WASHINGTON:** KITTATAS CO: Miller Pk.–NE slope, *Kruckeberg 3955* (RM 259527); **WASHINGTON:** KITTATAS CO: Iron pk trail, *Kruckeberg 2561* (IM 81739); **WASHINGTON:** KITTATAS CO: Fish L., *JWThompson 10683* (ND–G 010495, US 1651535, MO 1080669); **WASHINGTON:** KITTATAS CO: slopes along Beverly cr, *JWThompson 8751* (ND–G 010496, GH, UC 502630); **WASHINGTON:** KITTATAS CO: Swank R. valley, canyon gulch, *Sharpless 273* (GH, MO 720036); **WASHINGTON:** KITTATAS CO: 2 mi. up Beverly cr. fr. confluence, *Meyer & Meyer 2239* (F 1584022, MO 1579022 758341); **WASHINGTON:** KITTATAS CO: upper Beverly creek canyon, *Kruckeberg 5028* (COLO 194297, UC M292491); **WASHINGTON:** KITTATAS–CHELAN CO: hd of Fourth, Hardscrabble & Bean creeks, *Kruckeberg 5518* (COLO 194293, UC M292486); **WASHINGTON:** OKANOGAN CO: nr Conconcully–Muckamuck lookout, *Bigelow 116* (MO 1009847, GH); **WASHINGTON:** OKANOGAN CO: Mt Bonaparte, *JWThompson 10955* (MO 1080566, US 1650603); **WASHINGTON:** OKANOGAN CO: along Salmon cr to Muckamuck lookout, *JWThompson 6956* (MO 1012091, GH, UC 470741); **WASHINGTON:** PEND ORIELLE CO: near Dalkeena, *JWThompson 9216* (UC 539690); **WASHINGTON:** PIERCE CO: Iron mtn, Mt Ranier N. Pk., *Weigand 2801* (MO 1144349, F 886312); **WASHINGTON:** YAKIMA CO: Mt aix, *JWThompson 15019* (GH, US 1889126, CAN 195194, MO 1202222, COLO 86185, UC 749564); **WYOMING:** Teton Pk., *Williams & Pierson 168* (MO 1015988); **WYOMING:** Big Horn mtn, *Moses* (NY);

WYOMING: Jennys L., NW Wyoming, *Eikenberry 36* (F 346411); **WYOMING:** SW Wyoming, *Rose 243* (US 48785, RM 68723); **WYOMING:** JOHNSON CO: Big Horns-Circle Pk, 2 mi W US 16, *C.L. Porter 7075* (NY); **WYOMING:** LINCOLN CO: near alpine Sheep mtns., *Payson & Armstrong 3451* (MO 914225, GH); **WYOMING:** LINCOLN CO: Jacksons Hole, *Payson & Payson 2285* (NY, MO 869176); **WYOMING:** SUBLETTE CO: N Horse creek Rd., 6.8 mi W Merna jctn, 4 mi W Sherman stn, Wyo range, *Shultz,Shultz,Shultz 2893* (IM 155421); **WYOMING:** TETON CO: Gros Ventre River, *Lichvar 540* (RM 315615); **WYOMING:** TETON CO: Gros Ventre River, *Lichvar 548* (RM 315604); **WYOMING:** TETON CO: Taylor Pk.,-Teton mtns, *Hall 11455* (UC 217307); **WYOMING:** TETON CO: Teton Pk -Cascade canyon trail, *Schreiber 1263* (UC 615551); **WYOMING:** WASHAKIE CO: Rte 16, Upper Lee creek, Big Horn mtns, *Pennell & Schaeffer 24328* (GH);

Senecio streptanthifolius Greene var. *borealis* (T. & G.) Bain

ALBERTA: E side Jasper lake, *Morton N.A4596* (CAN 359772); **ALBERTA:** Panther R., SW slopes Bear mtn, *Porsild & Breitung 16243* (CAN 293546); **ALBERTA:** Crowsnest pass, *Dawson 14781* (CAN 110451); **ALBERTA:** Columbia Icefield, 60 mi SE Jasper, *Scoggan 16449* (CAN 307593); **ALBERTA:** Ft Chipewyan, *Preble* (US 1622307); **ALBERTA:** Jasper townsite, *Porsild & Breitung 14456* (CAN 293545); **ALBERTA:** Athabasca R. lat 53 30', *Speedborough 19724* (CAN 110450); **ALBERTA:** Jasper , *Scamman 3122* (GH, US 1897287); **ALBERTA:** N. fk Sask. R., *Brown 925* (MO 851475, US 1101815); **ALBERTA:** below Wilcox pass, *Brown 1390* (MO 851477, GH); **ALBERTA:** Mt. Forget-me-not, *Macoun 22774* (F 251349); **ALBERTA:** vic. Talbot L., *Porsild 22365* (CAN 266388); **ALBERTA:** Sofa mtn, Waterton, *Breitung 17174* (F 1482864); **ALBERTA:** Columbia icefield, *Löve & Löve 6650* (CAN 238664, COLO 269012); **ALBERTA:** L. Beauvert, Jasper Pk Lodge, *Scamman 2397* (GH); **ALBERTA:** Ft Chipewyan, *Laing 68* (US 1240083);

ALBERTA: Astoria R., Jasper park, *Ostheimer 8* (GH); **ALBERTA:** 20 mi E of Jasper, *Porsild 21103* (CAN 288137); **ALBERTA:** Livingston falls–Kananaskis Rd., *Morton NA4655* (CAN 417684); **ALBERTA:** jctn. N. Sask. & Alexandra R., *Porsild & Breitung* (CAN 293547); **ALBERTA:** Livingston falls campground, Coleman, *Hermann 12764* (US 2233481); **ALBERTA:** Jasper Pk, Athabasca valley, *Porsild 21300* (CAN 258376); **ALBERTA:** Jasper, *Malte* (CAN 221923); **ALBERTA:** Ft Chipewyan, *Harper 90125* (CAN 110427); **ALBERTA:** Highwood R.–ranger stn, *Brinkman 3176* (MO 949050, GH); **ALBERTA:** Brule L., *Riley 83* (US 622619); **ALBERTA:** Porcupine hills, N of Cowley, *Malte & Watson 610* (COLO 204766, RM 280383, UC M309734, CAN 293468); **ALBERTA:** along Salt R. nr Pine L., *Raup 3386* (CAN 110430, GH); **ALBERTA:** Jasper park, *Laing 362* (CAN 110448); **ALBERTA:** Patricia L. Jasper, *Moss 4632* (CAN 236364); **ALBERTA:** N. of Moose L. ranger stn, *Raup 3385* (CAN 110429); **ALBERTA:** 2 mi SW Jasper, *Turner 5099* (CAN 196387); **ALBERTA:** near Cataract Creek, mile 59.4 – Kananaskis Hwy, *J. Bain 79027* (ALTA); **ALBERTA:** Cardinal River Valley, ca.1 mile from recreation area, *J. Bain 79031* (ALTA); **ALBERTA:** 20 mi. W. of Whitecourt in pine forest, *J. Bain 173* (ALTA); **ALBERTA:** Cline River, in cleared areas, above NE side of river, *J. Bain 79016* (ALTA); **BC:** 20 km. S. of Savona, *J. Bain 054* (ALTA); **BC:** approx. 8 mi. N. of Dease Lake along Hwy #37(Cassian Hwy), *J. Bain 131* (ALTA); **BC:** 22 mi. S. of Watson Lake, open sandy pine forest, *J. Bain 164* (ALTA); **BC:** Cathedral Prov. Pk. at km. 25 of Park road, *J. Bain 053* (ALTA); **BC:** approx. 25 mi. W. of Dease Lake on road to Telegraph Creek in open meadow, *J. Bain 126* (ALTA); **BC:** Telegraph Creek, E. of airstrip along roadside, *J. Bain 129* (ALTA); **BC:** 20 km. S. of Savona near streambank, *J. Bain 057* (ALTA); **BC:** roadside between 70 Mile House and Green Lake Park, *J. Bain 061* (ALTA); **BC:** BC Hwy #7 to Atlin, approx. 40 mi. N. of Atlin, *J. Bain 137* (ALTA); **BC:** peak of Mt. Pope, NW of Ft. St. James, *McCabe 7520* (UC 649312); **BC:** Sand creek, *M. Henry 972a* (GH); **BC:** Churn creek, Pavilion area, *Sugden 145* (IM 91990); **BC:** 1000' above head of Dease Lake , *McCabe 8715* (UC 662043); **BC:** Carson mtn.–Marble mtns, *JW & E. Thompson 303* (CAN 110452, MO 1233244, UC 749452, F 1481711); **BC:** Chezacut, *McCabe 673* (UC 542921); **BC:** Morichetown, *Kujala*

& Cajander (CAN 394153); **BC:** mi 523, ALCAN -E off Coal River, above river., *Calder & Gillett 25288* (UC M313306); **BC:** Coldwater R., *Dawson 26689* (CAN 110455); **BC:** Skagit valley, *Macoun 69362* (GH, CAN 110456); **BC:** Blackwater canyon, NW of Quesnel, *Grant 66-19* (IM 157191); **BC:** Ft. Fraser, 2 mi N railway stn, *Eastham 11858* (CAN 110950); **BC:** slopes Carson mt.-Marble mtns, *JW & E Thompson 303* (NY); **BC:** Grant creek, *Sugden 143* (IM 91988); **BC:** Mtns E. of Hope, *Dawson 14780* (CAN 110458); **BC:** mtn. N of Germansen landing, Omineca River, above timberline, *McCabe 7753* (UC 649314); **BC:** Cariboo-Watch L. & Flying U ranch, *Eastham 11585* (CAN 110951); **BC:** Telegraph creek, Dease R., *Dawson 14775* (CAN 153661); **BC:** Pavilion Lake, *Taylor & Lewis 18* (UC M015586); **BC:** peak of Mt. Pope, NW of Ft. St. James, *McCabe 7502* (UC 649311); **BC:** Mt. Pope, NW of Ft. St. James, *McCabe 7818* (UC 649313); **BC:** Clinton, *Hardy 15024* (UC 708901); **BC:** Telegraph Creek, *Cooper & Andrews 425* (F 742196); **BC:** Ocean falls-Ostsa L. quad-trail to Mt. Pope, Ft. St. James, *Whitehorn 392* (GH); **BC:** btwn Princeton & Penticton, *Scoggan 15086* (CAN 307597); **BC:** Itcha Mtn.,-26 mi. NE of Anahim Lake, *Calder,Parmalee,Taylor 20262* (UC M290803); **COLORADO:** Denver, *Wolf 558* (US 48799); **MONTANA:** Jack cr canyon, *Rydberg & Bessey 5266* (ND-G 062986, NY, CAN 195187, F 81934); **MONTANA:** Midvale, *Umbach 154* (F 191188, US 541500, RM 154897); **MONTANA:** Midvale, *Umbach 78* (F 191123, US 541440); **MONTANA:** nr Red Lodge, *Rose 79* (US 48787, RM 68721, RM 68721); **MONTANA:** vic Cracker L. -Glacier park, *Standley 15853* (US 1027346); **MONTANA:** CARBON CO: Beartooth mtn, 20 mi SW Red Lodge, *Stolze 1018* (F 1641626); **MONTANA:** CARBON CO: Red Rock canyon, Custer NF, *Williams & Williams 3589* (ND-G 010487, MO 1123970, GH); **NWT:** Mi 103 -Enterprise-Mackenze R. hwy, *Thieret & Reich 6865* (CAN 275349); **NWT:** 5 km SE of Ft. Smith, *J. Bain 065* (ALTA); **NWT:** Moraine L., Gt SL. L., *W.H.Lewis 476* (US 2097176); **NWT:** Yellowknife, *Cody & McCanse 2345* (US 2034086); **NWT:** S camp, Taltson R., *Scotter 3187* (CAN 275206); **NWT:** Caribou Is., Gt Sl. L., *Seton & Preble 78581* (CAN 110445); **NWT:** btwn Jones Pt. & Ft Rae, Gt Br. L., *Bedford* (CAN 268128); **NWT:** Fairchild Pt., *Raup 1425* (CAN 279692); **NWT:** Mi 19 -Enterprise-Mackenze R. hwy,

Thieret & Reich 4875 (US 2344075, CAN 298395); **NWT:** Yellowknife, Joliffe Is., *Cody & McCanse 2477* (ORE); **NWT:** Ft Smith, *Taylor 14790* (CAN 110425); **NWT:** Fairchild Pt. Gt Slave L., *Raup 1426* (GH); **NWT:** Conjuror Bay, Gt Bear L., *Porsild & Porsild 3610* (CAN 110441); **NWT:** Ft. Smith, *Raup 1424* (CAN 279691); **NWT:** 1 mi W. Ft. Smith, *Cody & Loan 3805* (COLO 71963); **NWT:** Mc Tavish arm, Gt. Bear L., *Porsild & Porsild 3759* (CAN 110438); **NWT:** S. entrance to Conjuror Bay Gt Bear L., *Porsild & Porsild 3638* (CAN 110440); **NWT:** 1 mi. W. Ft. Smith, *Cody & Loan 3800* (US 2097447); **NWT:** Gordon L., *Henderson 27* (CAN 110437); **NWT:** McTavish arm, Gt. Bear L., btwn Labine Pt. & Glacier Bay, *Shacklette 2785* (F 1475875, US 1947342, CAN 200087); **NWT:** Ft. Smith, *Seton & Preble 78580* (CAN 110421); **NWT:** Yellowknife, *Cody & McCanse 2271* (ORE); **NWT:** Sawmill Bay, Gt. Br. L., *Corcoran 1* (MO 1637881); **NWT:** km. 154 - Hwy#1, 45 mi. W. of Enterprise, roadside, *J. Bain 071* (ALTA); **NWT:** Mackenzie R. N. fk., Nahanni R., *Wynne-Edwards 8527* (CAN 110434); **NWT:** Togun R., btwn L. Athabasca & Gt. Sl. L., *Harper 90129* (CAN 110426); **NWT:** shores of Gt. Sl. L., *Howe 1065(91998)* (CAN 110447); **NWT:** along abandoned roadside ca.40km W. of Ft. Smith in young pine stand, *J. Bain 067* (ALTA); **NWT:** Yellowknife R.-Gordon L., *Carroll 71* (CAN 110442); **NWT:** Mc Tavish arm, Gt Bear L., *Porsild & Porsild 3737* (CAN 110439); **NWT:** W. of Ft. Smith, *Cody 4029* (RM 233237); **NWT:** 64° 30' N 115°-117° W, *Lord 19* (CAN 110433); **NWT:** Gt Slave L. base Maufelly Pt., *Raup 1428* (CAN 311048, GH); **NWT:** Gt Bear L., Sawmill Bay, *Shacklette 2985* (CAN 200086); **NWT:** Mi 107.5 -Enterprise-Mackenze R. hwy, *Thieret & Reich 7090* (CAN 275350); **NWT:** Taltheilei narrows, Gt Slave L., *Raup 1427* (CAN 311049, GH); **NWT:** Fairchild Pt., Gt Sl. L., *Raup 1430* (GH); **NWT:** Windy Pt., Gt. Sl. L., *Howe 102688* (CAN 110446); **NWT:** Liard R. btwn Nahanni butte & Simpson, *Crickmay 122* (CAN 110435); **NWT:** Gt. Bear L., Pt. Radium, *Porsild 17156* (CAN 128173); **NWT:** btwn Wrigley & Blackwater R., *Crickmay 141* (CAN 110436); **UTAH:** Thousand L. mtn, *Ward 366* (F 577308, GH); **UTAH:** territories, *Ward 505* (F 106601); **UTAH:** Dyer mine, Uinta mtns, *Goodding 1331* (RM 41646); **UTAH:** GARFIELD CO: 22 mi N Escalante, along rd to Bicknell, *Holmgren, Reveal & LaFrance 2516* (BYU

56740, NY, IM 16041); **UTAH:** GARFIELD CO: 2 mi N Posey L., *Maguire 19202* (IM 104995, NY); **UTAH:** GARFIELD CO: 2 mi N Cyclone L.–Aquarius plateau, *Maguire 19256* (IM 104994); **UTAH:** GARFIELD CO: Iron spgs draw–Escalente mtns, *Reese 937* (IM 158958); **WYOMING:** E of Big Horn mtn., hd Clear cr & Crazy woman cr, *Tweedy 3027* (NY); **WYOMING:** Yellowstone Lake, Stevenson Island, *D'Evelyn & Fried* (UC 631645); **WYOMING:** Helton's Ranch, *Osterhaut 1838* (RM 155103); **WYOMING:** BIG HORN CO: *Dorn 3330* (RM 319671); **WYOMING:** BIG HORN CO: hd midfork Powder R., *Goodding 302* (NY, MO 1719529, US 485166, GH); **WYOMING:** BIGHORN CO: Ten Sleeps L., *Goodding 414* (F 215583, MO 1719530, US 485236, GH, NY); **WYOMING:** CARBON CO: Encampment–riverbottoms, *Tweedy 4130* (NY, US 432229); **WYOMING:** JOHNSON CO: Big Horns–nr Soudough cr, *Williams & Williams 3120* (NY, MO 1113207 1109796, RM 177302, GH); **WYOMING:** JOHNSON CO: Big Horn mtns nr hd Crazy Woman cr., *Porter & Porter 9385* (NY, GH, UC M221958); **WYOMING:** SHERIDAN CO: Big Horn mtn, *Tweedy 2085* (NY); **WYOMING:** SHERIDAN CO: S Tongue R. nr mouth Marcum cr., *Williams & Williams 3104* (NY, MO 1113205 1109797, GH); **WYOMING:** TETON CO: Crystal Creek– Gros Ventre Mtns., *Lichvar 673* (RM 315607); **WYOMING:** TETON CO: hoback canyon, *Wehmeyer, Martin & Loveland 5464* (NY, MO 1244197); **YUKON:** Klondyke, *Maclean* (US 669827); **YUKON:** Canol Rd., Lwr. Ross R., *Porsild & Breitung 9702* (CAN 110459, UC 994746); **YUKON:** Whitehorse– E. Lewes R., *Porsild & Breitung 9232* (CAN 110460); **YUKON:** km. 150, Skagway–Whitehorse Road, *J. Bain 79001* (ALTA); **YUKON:** 18.3 km. S. of Carcross bridge on Skagway Hwy., *J. Bain 79003* (ALTA); **YUKON:** km. 9 – Hwy#6 – between Tagish & Jake's Corners, *J. Bain 138* (ALTA); **YUKON:** Whitehorse, *M. Porsild 125* (CAN 110715); **YUKON:** Whitehorse, *Bayne-Beauchamp 123* (UC 488113); **YUKON:** lower Canol Rd., *M. Porsild 331* (CAN 110714); **YUKON:** lower Canol Rd., *M. Porsild 330* (CAN 110461); **YUKON:** km. 45.5, S. Canol Road, along the roadside, *J. Bain 79012* (ALTA); **YUKON:** 2 mi. N. of Carcross on Hwy#2, *J. Bain 139* (ALTA);

Senecio streptanthifolius Greene var. *rubricaulis* (Greene) Bain

CALIFORNIA: Lady Bug pk., *Leiberg 5318* (US 610567); **CALIFORNIA:** MONO CO: *Shockley* (F 374230); **CALIFORNIA:** MONO CO: hd Crooked creek,-White mtns, Inyo NF, *Maguire & Holmgren 26135a* (GH); **COLORADO:** ROUTT CO: Steamboat springs, *Goodding 1621* (BYU 193059); **COLORADO:** Grizzly creek, *Baker* (MO 1719531); **COLORADO:** nr Mountain falls around Pikes pk, *Bessey* (NY); **COLORADO:** EAGLE CO: Minturu, *Osterhaut 2559* (NY, RM 155045); **COLORADO:** EAGLE CO: Deep cr., *Killip 36450* (US 1829027); **COLORADO:** GARFIELD CO: nr Glenwood spgs, *Palmer 38121* (MO 1001170, GH); **COLORADO:** GUNNISON CO: Sapinero, *Baker 180* (MO 53295, GH); **COLORADO:** JACKSON CO: Kings canyon, *Payson & Payson 4288* (MO 932869); **COLORADO:** ROUTT CO: Steamboat spgs, *Goodding 1621* (NY); **IDAHO:** 25 mi. NE of St. Anthony, Big Bend Ridge, *Swisher 22* (COLO 42972); **IDAHO:** Victar, *Merrill & Wilcox 999* (US 581096); **IDAHO:** BANNOCK CO: Mink creek canyon, 5 mi. S. of Pocatello, *Lingenfelter 731* (UC, UC M163439); **IDAHO:** BANNOCK CO: Pebble creek, *Cronquist 254-36* (IM 46325); **IDAHO:** BANNOCK CO: Pebble creek, *Cronquist 241-36* (IM 46326); **IDAHO:** BANNOCK CO: 11 mi SW Pocatello, *Christ & Christ 18551* (NY); **IDAHO:** BANNOCK CO: Scout mtn., nr Pocatello, *Cronquist 312-36* (IM 46327); **IDAHO:** BONNEVILLE CO: Big Hole mtns., tie canyon, 6 air miles S. of Victor, *Holmgren & Mattala 5372* (COLO 257152); **IDAHO:** BONNEVILLE CO: Caribou mtn., *Payson & Armstrong 3520* (MO 914229); **IDAHO:** BONNEVILLE CO: Caribou city-NE slope of mtn, *Holmgren & Martala 5459* (BYU 106792, IM 132981, MO 1719798, US 508890, GH); **IDAHO:** BONNEVILLE CO: along Pine creek, W.of Victor, *Cronquist & Davis 2115* (MO 1180466); **IDAHO:** BONNEVILLE CO: Caribou range-Hoffman campgrd, *N. Holmgren 5533* (NY, IM 132980); **IDAHO:** BONNEVILLE CO: Tie canyon, 6 airmi. SW Victor, *N. Holmgren 5372* (NY, IM 132983); **IDAHO:** ELMORE CO: 4 mi N Featherville, along Red Warrior cr., *Baker 10431* (NY); **IDAHO:** FREMONT CO: sawtelle, *Christ 5758* (NY); **IDAHO:** FREMONT CO: 14 mi N Macks Inn below Targhee Pk., *Christ & Christ 19001* (NY); **IDAHO:** OWYHEE CO: Wilson, *Tucker 727* (NY); **IDAHO:** POWER CO: jctn of Bull and Big canyons,

Foster 6434 (BYU 184711, RM 314726, NY); **IDAHO:** TETON CO: Victor mtn S.of town, *Christ 5311* (NY); **IDAHO:** TWIN FALLS CO: Shoshone ranger stn, *Gierisch 697* (IM 32948); **NEV:** WHITE PINE CO: Wh. Pine mtn-ridgeE of Currant mtn, *Holmgren,Reveal,LaFrance 2186* (BYU, IM 116039 56742); **NEVADA:** Mountain city, *Nelson & Macbride 2201* (US 544955, MO 712268, IM 55107, RM 75468); **NEVADA:** Caliente-slopes, *Tidestrom 9495* (US 1329142); **NEVADA:** CO: Rattlesnake canyon-near Lee PO, *Heller 9554* (GH); **NEVADA:** ELKO CO: Sheep cr -Indepedence mtns, *Tiehm & Birdsey 5236* (IM 165378); **NEVADA:** ELKO CO: W. side of Ruby Lake, *Mason 4659* (UC 566642); **NEVADA:** ELKO CO: *Greene* (ND-G 063317); **NEVADA:** ELKO CO: nr Deeth, Ruby mtns, *Heller 9091* (F 282982, GH); **NEVADA:** ELKO CO: Rattlesnake canyon nr Lee PO, *H 9554* (F 251938); **NEVADA:** ELKO CO: *Greene* (ND-G 063318); **NEVADA:** ELKO CO: near Jarbidge at Bear Creek Meadows, *J. Bain 207* (ALTA); **NEVADA:** ELKO CO: Spruce mtn, *Holmgren 1507* (IM 48058); **NEVADA:** ELKO CO: nr Deeth, Clover mtns, *Heller 9091* (F 251934); **NEVADA:** ELKO CO: Favre L., *Mills & Beach 1309* (UC M035627); **NEVADA:** ELKO CO: S fk Long creek, *Borell* (IM 94088); **NEVADA:** ELKO CO: nr summit Copper mtn, *Maguire & Holmgren 22337* (NY); **NEVADA:** ELKO CO: *Greene* (ND-G 063319); **NEVADA:** ELKO CO: *Train 594* (ND-G 010485, UC 831695); **NEVADA:** ELKO CO: Gold Creek, *Kennedy 4392* (UC 190186); **NEVADA:** ELKO CO: Copper mtn-nr summit, *Maguire & Holmgren 22337* (US 1924046, IM 56045, GH); **NEVADA:** WASHOE CO: Hunters cr Rd., 9-11 mi SW Reno, *Archer 6282* (F 1484000, UC 831694, MO 1183435); **NEVADA:** WHITE PINE CO: S Ruby mtns- Sherman mtns, *Holmgren & Bethers 3901* (IM 132984); **NEVADA:** WHITE PINE CO: White Pine mtns-ridge leading E. of Currant Mt., *Holmgren,Reveal & LaFrance 2186* (NY); **NEVADA:** WHITE PINE CO: S Ruby mtns- Sherman mtns E slope, *N.Holmgren 3901* (NY); **U:** SUMMIT CO: E. of Hoyt's Peak, *Welsh & Murdock 12485* (BYU 124982); **UTAH:** Wasatch, *Clos 72* (US 855318); **UTAH:** , *Rydberg & Carleton 7467* (NY); **UTAH:** Alta, Wasatch mtns, *MEJones 1125* (F, F 397063); **UTAH:** Big cottonwood canyon, below Silver L., *Rydberg & Carleton 6344* (NY); **UTAH:** Aquarius plateau, hd Poison cr, *Rydberg & Carleton 7430* (NY); **UTAH:** XL canon, San Pitch mtns,

Wasatch?, *Tidestrom 1292* (US 506683); **UTAH:** Alta, Wasatch mtns, *M.Jones 1125* (GH); **UTAH:** Mt Majestic-hd Big Cottonwood canyon, *Rydberg 6829* (NY); **UTAH:** Silver Lake-Big Cottonwood canyon, *Clemens* (UC 831614); **UTAH:** Provo, Wasatch mtns, *Goodding 1115* (RM 42590); **UTAH:** Provo, *Goodding 1115* (MO 1719734); **UTAH:** Mt Terrell, *Tidestrom 1828* (US 1602221 507922); **UTAH:** Wasatch mtns, *S. Watson 669* (NY, US 48780, GH); **UTAH:** CACHE CO: Mt Naomi, *Maguire 14230* (IM 197299, NY); **UTAH:** CACHE CO: 20 mi NE of Logan, above Tony Grove L., *Cronquist 984* (MO 1180898); **UTAH:** CACHE CO: vicinity of Naomi Pk., *J. Bain 078* (ALTA); **UTAH:** CACHE CO: Logan canyon-old Juniper camp, *Maguire 13832* (IM 33100 32949 33466, US 1785043, GH, RM 186647 186579); **UTAH:** CACHE CO: 2 mi E Mantua, *Maguire 13813* (IM 33102, GH, RM 186649); **UTAH:** CACHE CO: Bear R.range,above Tony Grove L., *Maquire 16044* (NY); **UTAH:** CACHE CO: USAC campus, Logan-path from Main bldg., *Cronquist 930* (MO 1181444); **UTAH:** CACHE CO: Mt. Baldy, *Snell* (IM 36120); **UTAH:** CACHE CO: Logan, *C.P.Smith 2208* (F 287721); **UTAH:** CACHE CO: W Hodges pasture-Logan canyon-Bear R. range, *Passy 69* (IM 21143); **UTAH:** CACHE CO: W Hodges pasture-Bear R. range, *Passy 8* (IM 21142); **UTAH:** CACHE CO: Logan R., lowest dam, *Cronquist 536-A-37* (IM 46328); **UTAH:** CACHE CO: Dry canyon, *Maguire 13829* (IM 33101, US 1785042, GH, RM 186648); **UTAH:** CACHE CO: nr Tony Grove L., *Breedlow* (IM 144725); **UTAH:** CACHE CO: Rte #2 Logan-Garden city hwy., *Snell* (IM 36113 36130); **UTAH:** CACHE CO: Bear R. range, above Tony Grove L., *Maquire 16044* (BYU 46122, IM 119432); **UTAH:** CACHE CO: Logan, *C.P.Smith 2207* (F 287720); **UTAH:** CACHE CO: W hodges pasture, 1 mi below Tony grove ranger stn, *L.Allen* (IM 32950); **UTAH:** CARBON CO: 20 mi N Wellington, hd L fk Minnie Maud creek, *Maguire 18561* (IM 120073); **UTAH:** CARBON CO: 20 mi N Wellington, W. Tavaplats plateau, *Maguire 18533* (IM 120072, NY); **UTAH:** CARBON CO: Pine canyon-N Wellington, N side Book cliff mtn, *Graham 8311* (GH); **UTAH:** CARBON CO: 20 mi N Wellington, Minnie Maud cr, *Maquire 18561* (NY); **UTAH:** DAGGETT CO: Hickerson park, *Jensen* (IM 62680, GH); **UTAH:** DAVIS CO: Top Farmington canyon,Chicken cr watershed, *Clark 490* (IM 113277); **UTAH:** DAVIS CO: Farmington canyon, above

L., *Clark 1449* (IM 133956); **UTAH:** DUCHESNE CO: N of 3rd Chain L., *Graham 8586* (GH); **UTAH:** DUCHESNE CO: E trib. Red Creek, *Graham 9408* (MO 1123777, GH); **UTAH:** DUCHESNE CO: 10 mi NE Castlegate, 2 mi W Indian canyon pass, *Graham 9490* (MO 1123776); **UTAH:** DUCHESNE CO: SW Moon L., *Graham 9335* (MO 1123758); **UTAH:** DUSCHESNE CO: lower edge of aspen, Uinta River canyon, *Graham 8049* (UC 832054); **UTAH:** DUSCHESNE CO: Mirror L., *B. Richards 4327* (IM 5534); **UTAH:** DUSCHESNE CO: W. Moon L., *Graham 6469* (F 884658); **UTAH:** GARFIELD CO: E sl Mt. Helen, Henry Mtns, *Maguire 19328* (BYU 45941); **UTAH:** GRAND CO: Post canyon, book cliff, *Graham* (MO 1123774); **UTAH:** GRAND CO: Post canyon, *Graham 9907* (F 884655); **UTAH:** JUAB CO: Lower Chicken Cr.–Gunnison Plateau, *Lewis 5229* (BYU 190929, IM 155712); **UTAH:** KANE CO: 15 mi. W of Orderville, *Maguire 18803* (BYU 36902, NY, IM 120649, GH, UC M249495); **UTAH:** RICHMOND CO: *Reese 489* (IM 153105); **UTAH:** RICHMOND CO: above Bear Lake, W. of Garden City in cmpgrd., *J. Bain 079* (ALTA); **UTAH:** RICHMOND CO: *Reese 315* (IM 159043); **UTAH:** SALTLAKE CO: *Garrett 2726a* (NY); **UTAH:** SALTLAKE CO: City cr canyon, *Garrett 2384* (F 246175, GH); **UTAH:** SALTLAKE CO: Cottonwood canyon, *Wann 3882* (IM 13789); **UTAH:** SALTLAKE CO: Salt L. city–Kimballs, *Clemens* (GH); **UTAH:** SALTLAKE CO: Red Butte canyon, *Garrett 1854* (F 246171, RM 56682); **UTAH:** SALTLAKE CO: City Cr canyon, *Garrett 2384* (NY); **UTAH:** SALTLAKE CO: Salt L. city–City creek canyon, *Clemens* (GH); **UTAH:** SALTLAKE CO: Parleys canyon, *Garrett 1805* (F 246170); **UTAH:** SALTLAKE CO: Red Butte canyon, *Garrett 1854a* (F 246172, GH, RM 56683, GH, NY); **UTAH:** SALTLAKE CO: Red Butte canyon–Wasatch mtns, *Arnow 1525* (NY); **UTAH:** SALTLAKE CO: E of Brighton Guard Stn, Big cottonwood canyon, *Eyre* (NY); **UTAH:** SALTLAKE CO: Parleys canyon, *Garrett 1805* (F 246169); **UTAH:** SALTLAKE CO: Salt L. city, red butte canyon, *Smith 1908* (IM 13874); **UTAH:** SALTLAKE CO: Salt L. C., *MEJones 1996* (F 475778); **UTAH:** SEVIER CO: W of Musinia Ranger stn, *Jeffery* (IM 101875); **UTAH:** SEVIER CO: 6.5 mi SSE Glenwood, Monroe mtns., *Welsh, Welsh & Henroid 17567* (BYU 185949, IM 155376); **UTAH:** SUMMIT CO: Burntfork cr, *Jensen* (NY, UC 704102, BYU 18859); **UTAH:** SUMMIT CO: nr Bear R., *Goodman 1860* (NY,

MO 1013596, US 1568139, GH, RM 154903); **UTAH:** SUMMIT CO: SW slopes of Bald mtn, *Maguire, Richards, Maguire 4326* (RM 140747, UC 533012); **UTAH:** SUMMIT CO: 12 km. W. of Elizabeth Pass, *J. Bain 084* (ALTA); **UTAH:** SUMMIT CO: N of Fish L., *Harrisons 10964* (US 1898496); **UTAH:** SUMMIT CO: 3 mi N China Mead, W. of road, *Lewis 6477* (IM 170207); **UTAH:** SUMMIT CO: Deadman mtn, Uintas, *Greenman & Greenman 4712* (MO 1008417); **UTAH:** SUMMIT CO: ca. 2 km E. of Elizabeth Pass, *J. Bain 083* (ALTA); **UTAH:** SUMMIT CO: Stillwater fk., Bear r., *Payson & Payson 4966* (MO 974306); **UTAH:** SUMMIT CO: Lamotte pk, *Hermann 5977* (MO 1244029); **UTAH:** SUMMIT CO: btwn S. fk Weber R.and Hoyts canyon, *Welsh & Murdoch 42485* (NY); **UTAH:** SUMMIT CO: Hewinta Pk, Wasatch NF, *147* (NY); **UTAH:** SUMMIT CO: S. of Lilly Lake & Lost Lake along Rte.150, *J. Bain 085* (ALTA); **UTAH:** SUMMIT CO: SW slope Bald mtn, *Maguire, Richards, Maguire 4326* (IM 5535); **UTAH:** SUMMIT CO: near E. fork of Bear River, Uintah mtns, *Goodman 1973* (RM 131164); **UTAH:** TOOELE CO: Strawberry mtn. S. willow canyon, *Taye 174* (NY, IM 160756); **UTAH:** TOOELE CO: E Hickman canyon, Stansbury mtns, *Taye 651* (IM 171200); **UTAH:** TOOELE CO: Vickopry mtn, Stansbury mtns, *Taye 526* (IM 171199); **UTAH:** UINTA CO: 2 mi N Vernal, *Goodman 3099* (MO 1230150); **UTAH:** UINTA CO: Uinta basin, nr Little L., *Graham 8256* (F 884661); **UTAH:** UINTAH CO: Chain Lakes Basin- 4th lake, *Welsh, Neese, Atwood 18960* (RM 318274); **UTAH:** UINTAH CO: Diamond valley, *Andrews, Noble* (IM 32947); **UTAH:** UINTAH CO: N.of Vernal, *Cottam 6041* (MO 1982789); **UTAH:** UTAH CO: Red rock canyon, near Salt L. city, *Rydberg 6064* (US 508562, RM 65817); **UTAH:** UTAH CO: Mt. Timpanogos, *Garrett 3544a* (RM 106908); **UTAH:** UTAH CO: Mt. Timpanogos, *Garrett 3568* (RM 106813); **UTAH:** WA CO: Zion pk., Overlook trail, *Nelson-9640* (IM 137273 145044); **UTAH:** WASATCH CO: base of Bear canyon, *Blauer & Brotherson 113* (NY); **UTAH:** WEBER CO: Mt. Ogden, *Clark 2217* (BYU 112359, IM 135488); **WYOMING:** Wasatch, *Watson 671* (GH, US 48781); **WYOMING:** Piney & Beaver cr, *Curtis 66605* (CAN 195195); **WYOMING:** Yellowstone-Golden gate, *Hawkins 540d* (US 1469446); **WYOMING:** Teton Pk., *Williams 1141* (IM 3528, MO 1063799, RM 135323); **WYOMING:** hdwaters Cliff cr, *Curtis* (NY); **WYOMING:** Yellowstone,-Electric pk, *Shear 179* (US 488758);

WYOMING: Jacksons hole, *Hayden* (MO 1719493); **WYOMING:** Teton Pk., *Williams 1758* (MO 1085308 1076979, IM 16921); **WYOMING:** Yellowstone, *Mearns 2719* (US 487280); **WYOMING:** Yellowstone- Excelsior geyser, *Hawkins 436a* (GH); **WYOMING:** Piney & Beaver creeks, *Curtis* (NY); **WYOMING:** Gros Ventre mtns, *Curtis* (NY); **WYOMING:** U.Buffalo fk to hd of Dunoir R., *Curtis* (NY); **WYOMING:** Grand Teton Natl Pk., *L. Williams 1141* (ORE); **WYOMING:** Mammoth hot spgs, *Mearns 3617* (NY); **WYOMING:** Mammoth hot spgs, *Mearns 2671* (NY, US 487250); **WYOMING:** LINCOLN CO: alpine on Snake R., *Payson & Armstrong 3399* (MO 914228, GH); **WYOMING:** LINCOLN CO: Jacksons hole, *Payson & Payson 2189* (NY, MO 869286); **WYOMING:** LINCOLN CO: 15 mi NE Cokeville, *Cronquist 8811* (NY, IM 101591, UC M249278); **WYOMING:** SUB CO: Piney mtn, 25 mi W. Big Piney, *Payson & Payson 2705* (F 559447, GH, US 1244253, MO 895595, UC 279568); **WYOMING:** SUBLETTE CO: Piney mtn-25 mi W. Big Piney, *Payson & Payson 2705* (NY); **WYOMING:** SUBLETTE CO: vic. Horseshoe Lake-w. slope Wind River range - SE of Pinedale, *Porter & Miller 6074* (UC 984231); **WYOMING:** SUBLETTE CO: nr Green R. lakes, *Porter 5555* (NY, GH); **WYOMING:** SUBLETTE CO: 25 mi W Big Piney 25 mi W. Big Piney, *Meyer & Meyer 2446* (NY, UC 758317, F 1584015, MO 1576244); **WYOMING:** TETON CO: Gros ventre R., *Williams & Pierson 689* (MO 1031861, GH); **WYOMING:** TETON CO: Granite Creek cmpgrd, 9 mi. N. of Hwy 187-189, N. of Bondurant, *J. Bain 106* (ALTA); **WYOMING:** TETON CO: vic teton pass, *Williams 781* (NY, MO 1031862, GH, IM 13790, RM 154845); **WYOMING:** TETON CO: 6 mi W Jackson, *Williams 3006* (NY, MO 1113209, GH); **WYOMING:** TETON CO: ca.10km. N. of Moran along roadside, *J. Bain 108* (ALTA); **WYOMING:** TETON CO: 10 mi. W. of Hwy.187-189 on Hwy#22 toward Teton Pass, *J. Bain 107* (ALTA);

Senecio oodes Rydberg

COLORADO: San Juan mtns- E. side Wolf Creek Pass, *Hall 11107* (UC 217254); **COLORADO**: Robinson, *Shear 3333* (US 856026); **COLORADO**: nr Breckinridge-Mt. Guyot, *Anderson* (MO 718571); **COLORADO**: Pitkin, *Clokey 2992* (MO 820398); **COLORADO**: Durango, *C.S.Crandell 3048* (NY); **COLORADO**: 7 mi W. of Placerville, *Kelly 1529* (COLO 57298); **COLORADO**: ARCHULETA CO: on road to Chimney Rock, via Devil creek, *Schmoll 1209* (COLO 11255); **COLORADO**: ARCHULETA CO: SE Pagosa Springs, -road to Chromo, *Weber & Livingston 6342* (COLO 93318); **COLORADO**: ARCHULETA CO: NE of Pagosa Springs, *Schmoll 1102* (COLO 11263); **COLORADO**: ARCHULETA CO: Pagosa spgs, *Bethel,Willey,Clokey 4391* (F 515570, MO 880556, US 1113895, UC 831966, ND-G 010491); **COLORADO**: ARCHULETA CO: SW jctn 160 & 84 -E. of Pagosa Springs, *Johnston 1245* (COLO 306640); **COLORADO**: EAGLE CO: Red Cliff, *Osterhaut 2703* (COLO 321801, NY); **COLORADO**: EAGLE CO: 7 km E. of Red Cliff on road to shrine, *J. Bain 105* (ALTA); **COLORADO**: GUNNISON CO: Parlius, *Eastwood* (COLO); **COLORADO**: HINSDALE CO: Lake City, *Ramaley 16489* (COLO 11265); **COLORADO**: HINSDALE CO: head of Indian creek -trail to Upper Powderhorn lake, *Weber 12145* (COLO 191857); **COLORADO**: LAKE CO: *Mosquin & Gillett 5363* (UC M287578); **COLORADO**: LAPLATA & SAN JUAN CO: Silverton, *Michener 325* (COLO 167870); **COLORADO**: LAPLATA & SAN JUAN CO: Silverton area, *Michener 387* (COLO 167869); **COLORADO**: LAPLATA & SAN JUAN CO: 18 mi. SE of Silverton, -Needle mtn quadrangle, *Michener 333* (COLO 167868); **COLORADO**: MINERAL CO: beside #160, 5 mi below Wolf cr pass, *Anderson & Barkley 2523* (NY); **COLORADO**: MINERAL CO: 2.6 mi below wolf cr pass, San Juan R.system, *Barkley & Anderson 2518* (NY); **COLORADO**: RIO GRANDE CO: E. side of Wolf Creek Pass by snowshed, along roadside, *J. Bain 096 & 096A* (ALTA);

COLORADO: SUMMIT CO: nr Breckinridge, *Mackenzie 154* (MO 2966997); **NEVADA:** ELKO CO: E Humboldt mtns, *Watson 668* (GH, US 48778); **WYOMING:** HUERFANO CO: 2 mi below Apishapa pass, *Barkley & Anderson 2451* (NY, MO 2500338); **WYOMING:** UINTA CO: nr Bear R., *Payson & Payson 4822* (US 1439689, MO 974495 974496, GH, RM 115231); **WYOMING:** UINTA CO: on Cty. Rd. 150, 2.5 km W. of Bear River and St. Rd. 150, *J. Bain 080* (ALTA);

Senecio laetiflorus Greene

CALIFORNIA: N. california, *Lemmon* (UC 335863); **CALIFORNIA:** Big valley, *Mrs Austin 2162* (NY); **CALIFORNIA:** Sierra nevada, *Lemmoir* (US 48715); **CALIFORNIA:** nr Boca, *Greene* (ND-G 063159); **CALIFORNIA:** SIERRA CO: Purdy, *Heller & Kennedy 8665* (F 222285); **CALIFORNIA:** SIERRA CO: 1.5 mi S. of Webber Lake, *Crum 1939* (UC 903106); **CALIFORNIA:** SISKIYOU CO: 2 mi. S. of Gazelle on road to Edgewood, *J. Bair 040* (ALTA); **CALIFORNIA:** SISKIYOU CO: Gazelle, *Heller 8076* (NY); **CALIFORNIA:** SISKIYOU CO: btwn Gazelle & Edgewood, *Heller 13670* (NY, MO 952353, US 1329417); **CALIFORNIA:** SISKIYOU CO: Gazelle, *Eastwood & Howell 1782* (MO 1081196); **CALIFORNIA:** SISKIYOU CO: Gazelle, *Heller 8076* (COLO 86998, UC 128685, F 192280, MO 1719564, US 611174, GH); **CALIFORNIA:** SISKIYOU CO: Shasta valley, btwn Gazelle & Edgewater, *Heller 13670* (F 585592); **CALIFORNIA:** SISKIYOU CO: HWY 99, 4 mi S. of Gazelle, *Baker 13076* (UC M037456); **CALIFORNIA:** SISKIYOU CO: margin of Grass Lake, *Ornduff 6269* (UC M169371); **IDAHO:** OWYHEE CO: 1 mi below NY summit, Silver City R., *Baker 8039* (NY); **IDAHO:** TETON CO: Teton gorge, tetonia, *Christ 5452* (NY); **NEVADA:** nr Carson city, *C.L. Anderson 188* (GH); **NEVADA:** Carson city, *M.Jones* (US 359610); **NEVADA:** CO: Hunters cr canyon, *Heller 10479* (UC 176498, F 384806, MO 1719561, US 509761, GH); **NEVADA:** WASHOE CO: Hunters cr canyon, *Heller 104792* (F 346522); **NEVADA:** WASHOE CO: Lemmon

valley, *Kennedy 2066* (MO 715497); **OREGON:** Harney valley, *Howell* (US 48810); **OREGON:** *Cusick 938* (F 182898, GH); **OREGON:** subalpine meadows, *Cusick 1617* (ND-G 062810); **OREGON:** Harney valley, *Howell* (NY); **OREGON:** S. Oregon mtns., *J. Howell* (F 182927); **OREGON:** nr Devine ranch, *Leiberg 2411* (F 462209, GH, US 276570, UC 175937, NY); **OREGON:** Annie creek, *Austin 1618* (US 667469); **OREGON:** near Silver L., *Leiberg 764 & 764a* (MO 1719563, GH, US 285752); **OREGON:** *Cusick 1617* (F 89471, MO 1719562, US 326141, UC 36035/ 91326); **OREGON:** Otis creek, *Leiberg 2324* (F 462150, GH, US 275640, UC 176455, NY); **OREGON:** Columbia R. opp mouth Deschutes R., *Howell 149* (US 49310); **OREGON:** CROOK CO: *Cronquist 7459* (NY, GH); **OREGON:** GRANT CO: along roadside, Hwy395, ca.25 mi. S. of John Day, *J. Bain 204* (ALTA); **OREGON:** GRANT CO: 4 mi W. of John Day, *19885* (UC 831871); **OREGON:** GRANT CO: 4 mi. W of John Day, *Peck 19885* (ORE); **OREGON:** HARNEY CO: 4 mi SE Burns, *Peck 18945* (MO 1285464); **OREGON:** HARNEY CO: 12 mi N. of Burns, *Peck 20114* (UC 693776); **OREGON:** HARNEY CO: 20 mi NW of Burns, *Peck 21039* (ORE); **OREGON:** HARNEY CO: Malheur Wilderness Reserve, *R.C. Erickson* (ORE); **OREGON:** KLAMATH CO: Beattie, *Peck 25476* (ORE); **OREGON:** KLAMATH CO: Modoc Pt., *Peck 15148* (ORE, NY, MO 949989); **OREGON:** KLAMATH CO: 2 mi N of Keno, *Peck 9393* (NY, MO, GH, ORE); **OREGON:** KLAMATH CO: 6 mi N of Ft Klamath, *Peck 19996* (NY); **OREGON:** KLAMATH CO: 3 mi. N. of Klamath Agency , *Peck 16817* (ORE, NY); **OREGON:** LAKE CO: 2 mi NW of Summer Lake , *Peck 20796* (ORE); **OREGON:** LAKE CO: 6 mi W. of Lakeview, *Peck 19645* (ORE); **OREGON:** LAKE CO: 8 mi W Lakeview, *Peck 15248* (MO 1042454 949988 , NY, ORE); **OREGON:** LAKE CO: Lakeview, *Peck 19642* (ORE); **OREGON:** MALHEUR CO: along Willow Cr. canyon, *Peck 7115* (ORE);

Senecio wallowensis Bain

NEVADA: WASHOE CO: Mt. Rose, *Heller 9896* (F 251942); **NEVADA:** WASHOE

CO: E. of Mt Rose on Jones cr trail, *Train 4393* (NY, IM 93619, UC 831974); **NEVADA**: WASHOE CO: nr Mt. Rose, *Howell 14176* (MO 1151297); **NEVADA**: WASHOE CO: Big meadows, *Williams, Howell, Tiehru, Gez, Lott 78-248-7* (IM 160777); **OREGON**: WALLAWA CO: near summit Pete's Peak, *Peck 17943* (UC 832102); **OREGON**: WALLOWA CO: Ice Lake, Wallowa Mtns., *J. Bain 199* (ALTA); **OREGON**: WALLOWA CO: Petes Pt., *G.Mason 1371* (ORE); **OREGON**: WALLOWA CO: steep slopes of Matterhorn, Wallowa Mtns., *G.Mason 1760* (ORE); **OREGON**: WALLOWA CO: steep mtn sides of Imnaha R., *Cusick 3131* (F 225018, MO 1719799, GH, NY); **OREGON**: WALLOWA CO: Ice L.,Wallowa Mt, *Peck 18514* (ORE, NY); **OREGON**: WALLOWA CO: Ice L., *Peck 18502* (ORE); **OREGON**: WALLOWA CO: high slope above Jewitt L., Wallowa Mt., *Peck 18055* (ORE); **OREGON**: WALLOWA CO: Ice L., *Ownbeys 1842* (F 1607597, US 1789882, MO 1211791, GH, RM 183640); **OREGON**: WALLOWA CO: Peets Pt.,Wallowa Mtn., *Peck 17961* (ORE); **WASHINGTON**: PIERCE CO: Iron mtn, Mt Ranier N. Pk., *Flett 3246* (MO 851663);

Senecio kluanei Bain

BC: W & NW slopes of Mt. Selwyn, *Raup & Abbe 4163* (CAN 110454, GH); **BC**: Taylor Flat–N. bank Peace R., *Raup & Abbe 3547* (GH, CAN 110453); **BC**: Chezacut, *McCabe 704* (UC 542928); **BC**: Clinton, *Macoun 14779* (CAN 110457); **YUKON**: 1 km. E. of Haines Jctn on Hwy #1 (Alaska Hwy), *J. Bain 152B* (ALTA); **YUKON**: km. 1538 – Alaska Hwy, W. of Whitehorse, *J. Bain 153* (ALTA); **YUKON**: 1 km. E. of Haines Jctn on Hwy #1 (Alaska Hwy), *J. Bain 152* (ALTA); **YUKON**: nr Stoney cr, Takhini R., *Michel 26* (US 2050150, GH, UC 674823); **YUKON**: 12 E Champagne, *Michel 21* (US 2050146, GH, UC 674824); **YUKON**: Lake Labarge – along roadside near the campground, *J. Bain 154* (ALTA); **YUKON**: Whitehorse, *Macoun 78961* (F 251955, CAN 153659);